Abstract. – A deepwater trapping survey for *Heterocarpus laevigatus* was conducted around the main islands of the Hawaiian Archipelago to estimate exploitable biomass and potential yield. Stratified sampling by depth zone and island was conducted over a 3-year period to evaluate shrimp catch rates. Catchability of the traps was estimated from a 12-day intensive fishing experiment performed at a small, isolated site in the Kaulakahi Channel; habitat areas were determined by digitizing nautical charts.

Results from a Leslie analysis of the depletion experiment showed that *H. laevigatus* is very susceptible to capture by traps (i.e., catchability q̂ = 9.48 ha/trap-night). There was no evidence of a change in size structure through the course of the experiment.

Shrimp catch rates varied greatly by island and depth of capture. Exploitable biomass was greatest in the 460–640 m depth range; negligible amounts of shrimp occurred shallower than 350 m and deeper than 830 m. Catch rates were highest at Niihau and lowest at Oahu. The total exploitable biomass of shrimp in the main Hawaiian Is. was estimated to be 271 MT, a figure substantially less than previously believed.

Analysis of multiple size-frequency distributions for each sex showed no evidence of modal size progression. Assuming equilibrium conditions, application of the Wetherall et al. (1987) method to these data resulted in estimates of $M/K = 1.01$ for female shrimp and 0.74 for males. From these results and estimates of L_∞ we calculate that $F_{0.1}/M = 0.75$ for females and 0.86 for males.

An assessment of the exploitable biomass of *Heterocarpus laevigatus* in the main Hawaiian Islands. Part 1: Trapping surveys, depletion experiment, and length structure

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The caridean shrimp, *Heterocarpus laevigatus* Bate 1888, is an abundant deepwater inhabitant of the Hawaiian Is., where it has been fished sporadically since 1970 (Anon. 1979). Two early research surveys (Clarke 1972, Struhsaker and Aasted 1974) showed that large catches of this species, and its smaller congener *H. ensifer*, could readily be taken in baited traps in water depths of 365–825 m (200–450 fm).* Based on catch rates from around the island of Oahu, the deepwater shrimp resource seemed sufficiently abundant to support a commercial fishery (2.6 kg/trap-night for *H. laevigatus* and 6.6 kg/trap-night for *H. ensifer*; Struhsaker and Aasted 1974).

To date, however, attempts to harvest the resource have met with limited success, even though 75 MT of *H. laevigatus* were landed by one vessel during a 14-month period (Tagami and Barrows 1988). At its peak in 1983–84, a short-lived fishery developed, involving as many as 7 medium-sized (23–40 m) boats. At that time over 190 MT of *H. laevigatus*

were landed, with an ex-vessel value of $1.5 million ($7.85/kg; Hawaii Dep. Land & Nat. Resour., Div. Aquat. Resour.). The fishery soon failed, however, primarily due to problems with gear loss, product processing, and localized stock depletions. Even so, the product was well received by the public, and rejuvenating the shrimp fishery remains a fishery development goal of the State of Hawaii (Anon. 1984).

With this interest in developing the Hawaiian fishery, major gaps in our knowledge of local *H. laevigatus* shrimp stocks have become apparent (see Gooding 1984, Dailey and Ralston 1986), although elsewhere in the Pacific more extensive data are available (e.g., Wilder 1977, King 1984 and 1986, Ralston 1986, Moffitt and Polovina 1987). Particularly lacking are estimates of the absolute abundance of the *H. laevigatus* stock in Hawaii and its ability to withstand sustained fishing pressure.

The primary objective of the work presented here was to estimate the exploitable biomass of *H. laevigatus* in the main Hawaiian Is. A secondary objective was to estimate growth and mortality rates through analysis of length-frequency data. Together

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*Depths are given in meters with fathom equivalents (1.0 fm = 1.83 m), although contouring and stratification were based on nautical charts in fathoms.

these findings could form a basis for estimating the potential yield of the shrimp resource.

To determine the exploitable biomass of shrimp at spatially discrete locations in Hawaii, the formula (Ricker 1975) was used:

$$CPUE = q \left[\frac{B}{A} \right]$$

where CPUE is the catch-per-unit-effort, q is the catchability coefficient of the fishing gear, B is exploitable biomass, and A is the area occupied by the population. This relationship is based on the explicit assumption that catch rate is strictly proportional to shrimp density (B/A), and that q is the proportionality constant equating these quantities. By rearrangement we have,

$$B = \frac{CPUE \cdot A}{q}.$$

Thus, to estimate the exploitable shrimp biomass at a locality we need (1) an unbiased estimate of catch rate, (2) a measure of the habitat area over which the catch rate prevails, and (3) knowledge of the sampling gear's efficiency (i.e., an estimate of q).

To accomplish these three objectives, the study was divided into two phases. First, a depletion experiment was conducted to estimate the catchability coefficient (q). This was followed by a depth-stratified sampling program for *H. laevigatus* around each of the main islands of the Hawaiian archipelago (i.e., Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau).

Methods

Shrimp trapping was conducted during a series of nine cruises of the NOAA ship *Townsend Cromwell* (Table 1). During each cruise, standard fishing gear was utilized to gather CPUE statistics at specific geographical locations. The gear employed was a top-loading pyramidal shrimp trap, identical in construction to those used commercially in Hawaii from 1983 to 1984. Each trap was made of welded steel reinforcement bars, had a 1.83 m² base, an overall volume of 1.84 m³, and was covered by 1.27 × 2.54 cm mesh hardware cloth. A full description and illustration of the gear is given in Tagami and Barrows (1988).

Typically, 6–10 solitary traps were set daily and allowed to soak overnight. Traps were generally deployed in the afternoon and hauled the following morning, being in the water for a period of 16–20 hours. All traps were baited with approximately 3 kg of chopped mackerel *Scomber japonicus*. After hauling to the sur-

face, each trap was emptied and the contents were sorted to species, counted, and weighed to the nearest 0.01 kg. Random subsamples of ~200 *H. laevigatus* were routinely collected, from which carapace length (CL) was measured to the nearest 0.1 mm using dial calipers. For all measured shrimp, sex was determined by examining the endopodite of the first pleopod (spatulate in males, pinnate in females; see King and Moffitt 1984). In addition, the ovigerous condition of females was recorded.

Depletion experiment

To estimate q, an intensive fishing experiment was conducted (see also Ralston 1986). Depletion experiments, including the Leslie method used here (Ricker 1975), have three restrictive assumptions. First, all individuals in the exploitable portion of the population are equally likely to be captured with the fishing gear. Second, the fished population is closed, or else additions exactly balance removals other than those due to fishing. Third, fishing removals account for all changes in stock biomass, such that natural mortality, growth, and recruitment have negligible effects during the period of fishing. Thus, the best site for a depletion experiment is a naturally isolated, small area so that removals can be carried out over as short a time-interval as possible.

A small rise midway in the Kaulakahi Channel (21° 54.5'N, 159°56.5'W) separating Kauai and Niihau was

Table 1
Summary of shrimp-trapping cruise dates and locations.

Date	Location	No. of traps hauled
April 1985	Molokai	3
	Lanai	1
May 1986	Kaulakahi Channel	105
July 1986	Kaulakahi Channel	10
Sept. 1986	Kaulakahi Channel	10
Nov. 1986	Kaulakahi Channel	12
Sept./Oct. 1987	Niihau	68
	Kauai	128
	Kaulakahi Channel	11
Feb./March 1988	Kaulakahi Channel	10
	Oahu	8
	Hawaii	31
Oct. 1988	Kaulakahi Channel	17
	Molokai	20
	Lanai	18
	Maui	38
	Kahoolawe	8
March 1989	Oahu	67
	Molokai	32

chosen for the work. This nearly circular rise (Fig. 1) with a crest at 421m (230fm), has an area of 1187ha (horizontal planar area <640m or 350fm) and is isolated from the Islands of Kauai and Niihau by depths >730m (400fm; Fig. 2). The site lies in the required depth range for *H. laevigatus* and has relatively high densities of the target species.
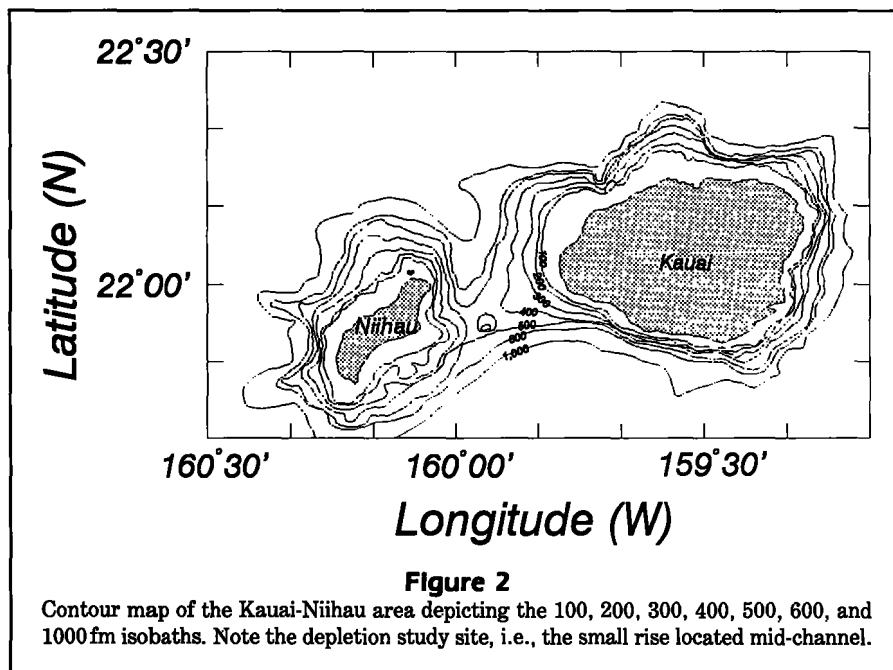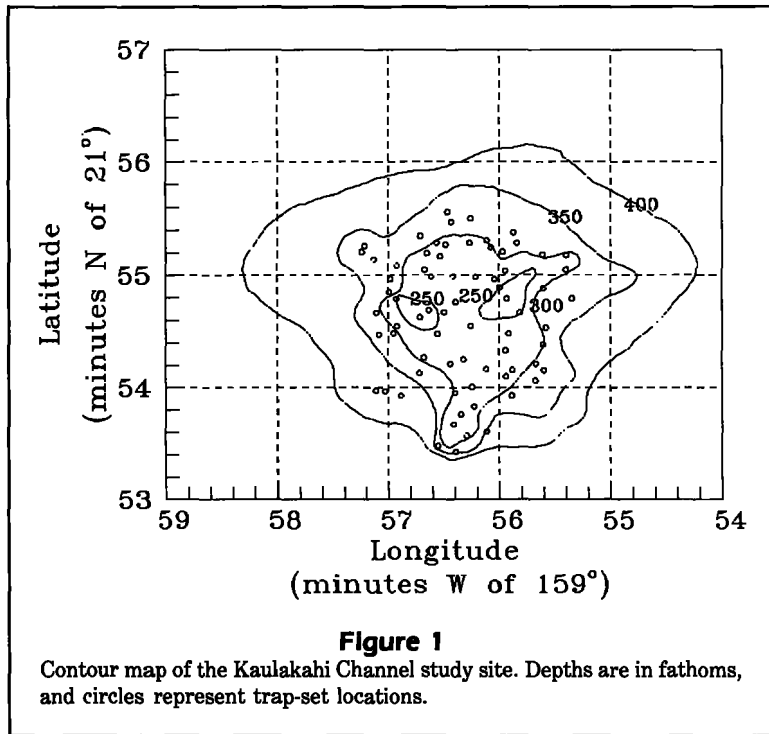
The intensive fishing experiment was conducted 13–24 May 1986. During each of the 12 days of the experiment, 6–14 pyramidal shrimp traps were set between depths of 421 and 695m (230 and 380fm). Following the Leslie method (Ricker 1975, Seber 1982), catchability was estimated directly from the slope of the linear regression of CPUE on corrected cumulative catch. That is,

$$CPUE_i = q \cdot B_i$$
$$= q(B_0 - K_i)$$
$$= qB_0 - qK_i,$$

where $CPUE_i$ is the catch-per-unit-effort on day i (kg/trap-night), q is the catchability coefficient/trap-night of the pyramid traps, B_i is the average biomass (kg) present on day i, B_0 is the biomass (kg) of shrimp present at the start of the experiment, and K_i is the corrected cumulative removals for day i, defined as

$$K_i = \frac{1}{2} C_i + \sum_{n=1}^{i-1} C_n,$$

where $C_n(n=1,2,\ldots,i)$ is the catch (kg) taken on each day of the experiment. Note that the estimate of catchability ($\hat{q}$) pertains strictly to the interaction between the traps we used and the stock resident in the study area, which is normalized to unit area after multiplying by 1187ha (i.e., the area of the study site).

Figure 1

Contour map of the Kaulakahi Channel study site. Depths are in fathoms, and circles represent trap-set locations.

Figure 2

Contour map of the Kauai-Niihau area depicting the 100, 200, 300, 400, 500, 600, and 1000fm isobaths. Note the depletion study site, i.e., the small rise located mid-channel.

Determination of habitat areas

The distribution of *H. laevigatus* is strongly dependent on bottom depth. Little or no shrimp occur in waters outside the 366–915m (200–500fm) range (Struhsaker and Aasted 1974, Gooding 1984, Dailey and Ralston 1986). In the main portion of the Hawaiian Archipelago (Hawaii, Maui, Lanai, Kahoolawe, Molokai, Oahu, Kauai, and Niihau) a number of islands share a common 915m (500fm) depth contour (e.g, Kauai and Niihau; Fig. 2). Even so, in our study each island was treated as a separate stock for

purposes of geographically stratifying the analysis. An exception was made for the islands of Maui, Lanai, Kahoolawe, and Molokai (MLKM), which share, in addition to the 915 m (500 fm) contour, a common 366 m (200 fm) isobath. These four islands were, therefore, treated as a single geographic locality.

Estimates of the amount of suitable shrimp habitat, in hectares (1 ha = 0.01 km²), were obtained by determining the horizontal planar area lying between charted depth contours. A large digitizing tablet was used to calculate all area estimates directly from nautical charts (NOAA charts 19016, 19019, and 19022, and Defense Mapping Agency bottom contour charts). These charts included 915 m (500 fm) isobaths, but we manually contoured all of the 366 m (200 fm) isobaths using the sounding data provided on each chart. In addition, good detailed bathymetry was available for the islands of Kauai and Niihau, and at these sites the 458 m (250 fm), 549 m (300 fm), 640 m (350 fm), 732 m (400 fm), and 824 m (450 fm) isobaths were contoured and digitized as well.

Each contour was digitized three times by each author, providing a minimum estimate of measurement error in our calculation of habitat areas. These errors were typically small (median CV 0.5%, range 0.1–1.9%). A potentially more serious type of error concerns discrepancies between the actual locations of contours and their representations on charts. However, we had no information concerning the magnitude of this type of error and, given that measurement errors were negligible, we assumed that our estimates of habitat area were accurate and precise.

These data were then used to calculate habitat areas for each 92 m (50 fm) depth interval between 366 and 915 m (200–500 fm). First, the relative distribution of habitat was calculated from the Kauai and Niihau data. To estimate depth-specific habitat areas for the three remaining sites (Oahu, MLKM, and Hawaii), the combined relative proportions of habitat for each depth interval obtained at Kauai–Niihau were applied to the estimates of total habitat area between 366 and 915 m (200–500 fm). In support of this procedure, results in Mark and Moore (1987) indicate that slope-depth relationships among the main islands of the archipelago are, in general, similar.

Depth-stratified sampling

For the second phase of the assessment, each of the island areas was targeted for comprehensive trapping surveys to determine abundance patterns (i.e., catch rate) with depth and to estimate standing stocks (Table 1). A depth-stratified sampling approach was used. From preliminary data gathered at Kauai and Niihau during the September 1987 cruise, the mean and vari-

ance in CPUE were calculated for each of the six 92 m (50 fm) depth intervals lying in the 366–915 m (200–500 fm) range. Based on the results of this vertical distribution survey, sampling effort was optimally partitioned into depth strata by Neyman allocation (Cochran 1977), i.e., trap allocations to each depth interval were based on the product of abundance (CPUE · habitat area) and the standard deviation of CPUE at that depth. As each cruise progressed, CPUE means and variances were recalculated daily and the trap allocation schedule was updated.

From the results of the surveys, exploitable biomass was estimated (Eq. 1) for each depth interval at each site visited. This calculation assumes that the catchability estimate, which was determined at the depletion experiment study site, can be extended to all other localities sampled. An estimate of the variance of the biomass for each stratum was obtained from Eq. 1 using the delta method (Seber 1982), resulting in

$$ \mathrm{VAR}[B] \approx \frac{A^2}{\hat{q}^2} \mathrm{VAR}[\mathrm{CPUE}] + \frac{A^2 \cdot \mathrm{CPUE}^2}{\hat{q}^4} \mathrm{VAR}[\hat{q}] $$

if all covariance terms are zero (a reasonable first assumption) and VAR[A] is negligible (see above). Confidence intervals were then calculated using the distribution of standard normal scores ($\alpha = 0.05$, $Z = 1.96$).

Length-frequency analysis

The Kaulakahi Channel experimental depletion site was visited on seven separate occasions during May 1986–March 1988 (Table 1). During each visit a length-frequency sample of *H. laevigatus* was obtained, with the ultimate goal of analyzing the progression of size modes over time (egg bearing is strongly seasonal; Dailey and Ralston 1986, Moffitt and Polovina 1987). Additional length-frequency samples were obtained during the course of the depth-stratified sampling at each of the island sites.

Mortality and growth parameters were estimated from length-frequency distributions using the regression method of Wetherall et al. (1987). This technique requires an equilibrium population size-structure, an undesirable and restrictive assumption. Even so, data are available to support its use. Dailey and Ralston (1986) present length-frequency data for male and female shrimp sampled during the earliest stages of the fishery (1983–84). The data are very similar to those presented here, suggesting that exploitation has yet to seriously affect size composition. Additionally, the time-invariance of the size-frequency data we collected at the Kaulakahi study site (see below) indicates equilibrium conditions.
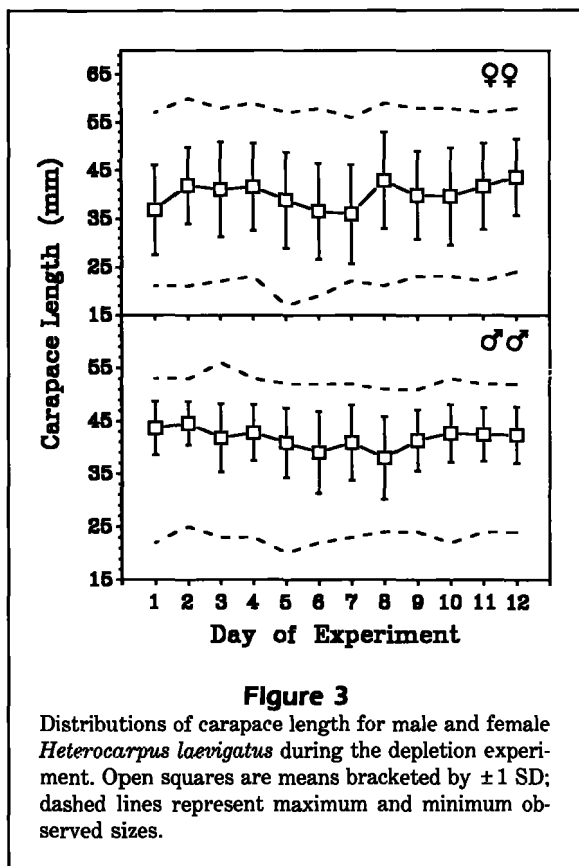
Figure 3
Distributions of carapace length for male and female *Heterocarpus laevigatus* during the depletion experiment. Open squares are means bracketed by ±1 SD; dashed lines represent maximum and minimum observed sizes.

Figure 4
Leslie model applied to the experimental depletion of *Heterocarpus laevigatus* at the Kaulakahi Channel study site. Each point represents one valid trap-night of fishing.

For each sex, the von Bertalanffy asymptotic length (CL_∞) and the ratio (Θ) of the total mortality rate (Z/yr) to the von Bertalanffy growth coefficient (K/yr) were estimated from a weighted regression of mean lengths $(CL_{\mu i})$ on full vulnerability cutoff lengths (CL_{ci}). In the analysis, the CL_{ci} were incremented in 1.0 mm steps above CL_{co}, the minimum size of full vulnerability to the gear, and the $CL_{\mu i}$ were recalculated at each step. Using the morphometric functional regressions presented in Dailey and Ralston (1986), CL_{co} was set equal to 30 mm (the length of *H. laevigatus* with carapace width = 12.7 mm), corresponding to the least dimension of the wire mesh covering the traps. This approach to estimating CL_{co} deviates from that used in previous applications of the regression method to *H. laevigatus* stocks. Dailey and Ralston (1986) and Moffitt and Polovina (1987) both assumed that shrimp were not fully selected by baited traps until reaching a CL greater than the modal size of length-frequency distributions from trap catches.

Because the size-structure we observed was similar to the unexploited stock (see above), it follows that $\Theta = M/K$, where M is natural mortality/yr. Likewise, using the length-weight regressions of Dailey and Ralston (1986), we estimated the asymptotic weights
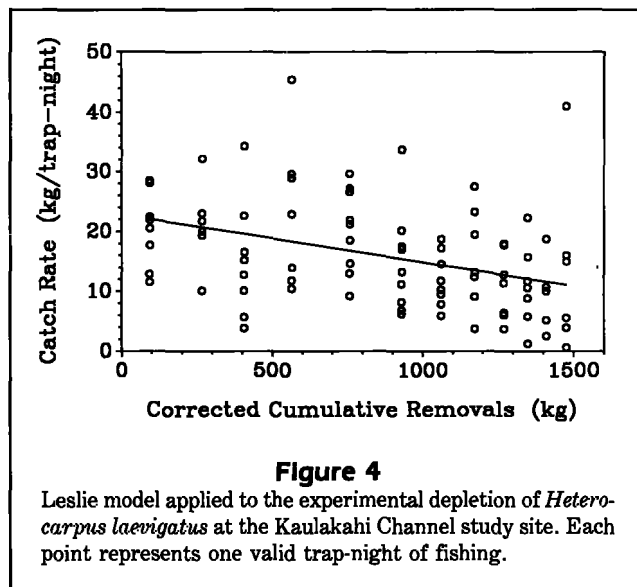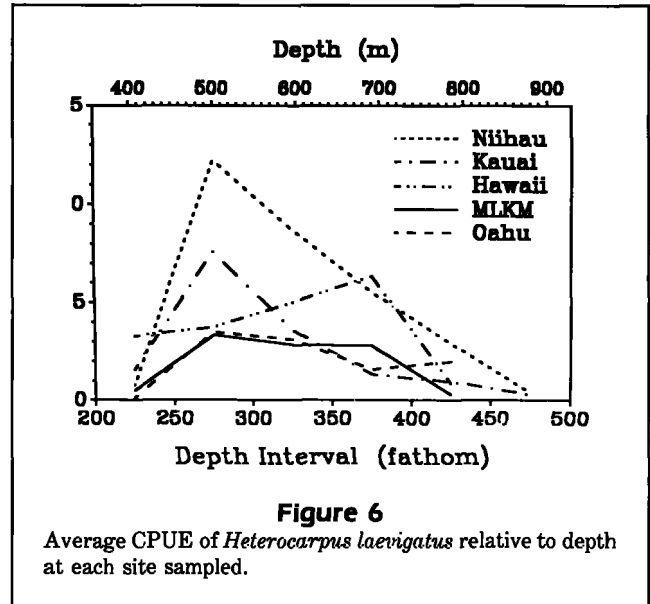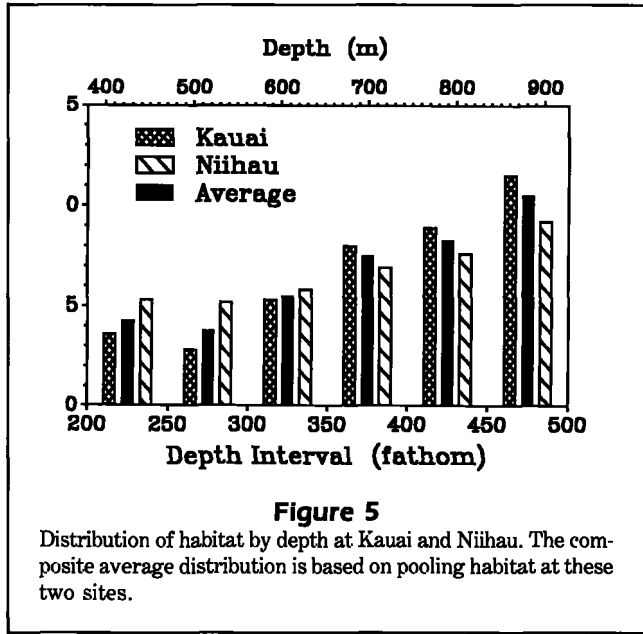
(W_∞) for each sex as the predicted weight at $CL = CL_\infty$. The average size at entry to the fishery $(CL_{p'}$ *sensu* Beverton and Holt 1957) was obtained by averaging the minimum size caught and CL_{co}. Given estimates of M/K, W_∞, and $CL_{p'}$, we used the tables presented in Beverton and Holt (1966) to determine sex-specific values of yield-per-recruit (Y/R) at various levels of exploitation (F/M). From these data we computed values of $F_{0.1}/M$, the exploitation level at which the marginal increase in Y/R declines to 10% of its value at the origin (Gulland and Boerema 1973, Gulland 1983).

Results

Depletion experiment

During the depletion experiment, 123 pyramid shrimp traps were set at the Kaulakahi Channel study site. Of these, 19 were lost, resulting in 104 effective trap-nights of standard fishing effort and a gear loss rate of 15%. A total of 45,482 *H. laevigatus* were caught, which collectively weighed 1499 kg. The average size of each shrimp was therefore 33.0 g. During the 12-day course of the experiment, no change occurred in the daily mean size of shrimp caught (Fig. 3; $r_\varphi = 0.32$, df 10; $r_\sigma = -0.28$, df 10).

Individual trap catches were regressed on values of corrected cumulative removals to date (Fig. 4). Traps that did not fish properly (e.g., the funnel entrance was ajar upon retrieval) were not included, although cumulative removals (K_i) included all shrimp caught in the study area (<695 m or 380 fm). Therefore, each point represents an observation of CPUE from one valid

Figure 5
Distribution of habitat by depth at Kauai and Niihau. The composite average distribution is based on pooling habitat at these two sites.

Figure 6
Average CPUE of *Heterocarpus laevigatus* relative to depth at each site sampled.

trap-night of fishing. Also presented is the ordinary least-squares regression equation relating these variables. The equation of the line is

$$CPUE_i = 22.84 - 0.007988[K_i],$$

with standard errors of the slope and intercept equal to 0.001997 and 1.9368, respectively. The regression is highly significant ($F_{1,89} = 16.00$, P 0.0001). The residuals show no obvious departure from linearity, an indication of constant catchability.

Under the Leslie model, the exploitable biomass at the start of the experiment is defined by the x-intercept, i.e., 2859 kg. Because the study site covered 1187 ha, this amounts to an initial density of 2.4087 kg/ha, which produced an initial catch rate ($CPUE_0$) equal to 22.84 kg/trap-night (i.e., the y-intercept). Then, $\hat{q}$ expressed on a hectare basis, rather than defined in terms of the study site, is estimated to be 9.4798 ha/ trap-night. In real terms, one overnight soak of a single, large pyramidal shrimp trap is estimated to have captured ~0.8% of the shrimp in the entire study area, which is equivalent to all the shrimp in ~9.5 ha, were they randomly dispersed. The standard error of $\hat{q}$/ha is the product of A (1187 ha) and the standard error of $\hat{q}$ measured over the study site (0.001997) (Seber 1982).

It is instructive to note that an initial density of 2.4087 kg/ha is equivalent to an average of 73 shrimp/ ha (see statistics for mean shrimp weight above). Based on this density, the average utilization of habitat by each shrimp was 137 m², a remarkable figure given

the relatively high catch rate encountered at the beginning of the depletion experiment (22.83 kg/trap-night).

Depth-stratified sampling

Habitat areas by 92 m (50 fm) depth intervals were estimated for the Oahu, Hawaii, and MLKM sites by assuming that the proportionate distribution of habitat between 366 and 915 m (200–500 fm) at these sites was the same as the composite distribution obtained at Kauai and Niihau. While there were some differences in the distribution of habitat with depth between Kauai and Niihau (Fig. 5, Table 2), they were relatively minor. At both sites the amount of habitat in the 458–549 m (250–300 fm) depth interval was slightly less than in the 366–458 m (200–250 fm) interval; but with increasing depth below that, the amount of habitat per 92 m (50 fm) depth interval increased steadily.

There were, however, marked differences in CPUE with depth among the five localities sampled (Fig. 6, Table 2). Catch rates at Niihau were particularly high relative to the other areas, especially at 458–549 m (250–300 fm). Catch rates at Oahu and MLKM were much lower. The modes of the distributions at Kauai and Niihau were shifted to the shallow end of the depth range, whereas at Hawaii it was shifted deeper.

Results presented in Table 2 provide estimates of the exploitable biomass (B), as well as variance estimates, for the depth intervals sampled at each site. Although catch rates at Niihau are quite high, the reduced amount of habitat at this island (69,530 ha) is sufficient to support only a small stock of shrimp (35.7 MT). Oahu, with its much lower catch rates, has a larger exploit-

Table 2
Depth-stratified sampling results for *Heterocarpus laevigatus* in the main Hawaiian Is.

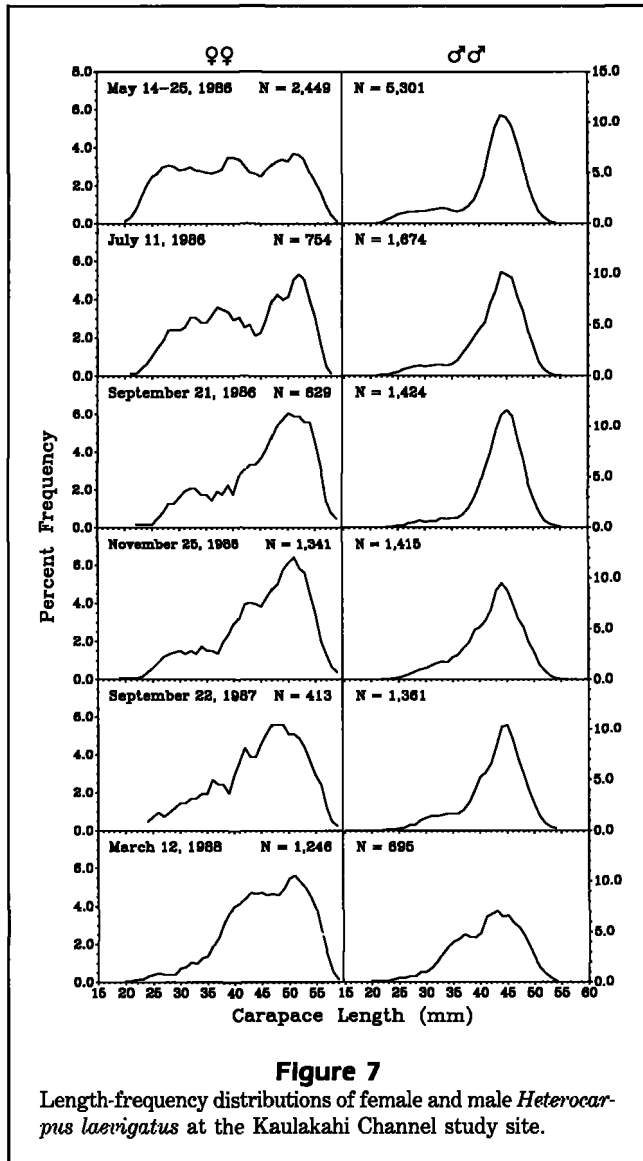| Depth range (m)	(fm)	No. traps set	Mean CPUE kg/trap	VAR[CPUE]	Habitat area (ha)	B (kg)	VAR[B]
Kauai							
366–458	200–250	29	1.566	0.894	12,760	2,108	1,897,271
458–549	250–300	37	7.587	1.093	12,070	9,663	7,608,356
549–640	300–350	25	3.607	0.322	14,410	5,481	2,621,353
640–732	350–400	18	1.324	0.436	16,940	2,367	1,742,930
732–824	400–450	6	0.953	0.203	17,770	1,786	912,472
824–915	450–500	7	0.299	0.038	20,200	637	197,960
Totals		122			94,150	22,042	14,980,342
Niihau							
366–458	200–250	9	0.788	0.586	10,670	887	791,140
458–549	250–300	18	12.214	7.253	10,570	13,611	20,586,349
549–640	300–350	19	8.719	3.335	11,010	10,127	10,907,759
640–732	350–400	10	5.533	2.737	11,730	6,847	7,120,644
732–824	400–450	4	2.903	0.906	12,210	3,739	2,377,052
824–915	450–500	4	0.380	0.094	13,340	535	204,092
Totals		64			69,530	35,746	41,987,037
Oahu							
366–458	200–250	6	0.122	0.017	41,570	535	342,588
458–549	250–300	20	3.482	3.239	40,100	14,726	71,490,061
549–640	300–350	33	3.115	0.480	45,070	14,810	24,568,526
640–732	350–400	13	1.594	0.698	50,800	8,542	24,613,230
732–824	400–450	2	1.990	0.303	53,300	11,187	17,379,858
824–915	450–500	0	0.000	0.000	59,510	0	0
Totals		74			290,350	49,800	138,394,264
Hawaii							
366–458	200–250	1	3.270	2.152	38,720	13,357	47,049,206
458–549	250–300	4	3.750	2.223	37,320	14,767	48,097,991
549–640	300–350	11	5.008	3.882	41,980	22,171	106,796,660
640–732	350–400	11	6.325	3.036	47,300	31,560	137,841,468
732–824	400–450	4	0.858	0.889	49,630	4,491	25,603,225
824–915	450–500	0	0.000	0.000	55,430	0	0
Totals		31			270,350	86,345	365,388,550
Maui-Lanai-Kahoolawe-Molokai							
366–458	200–250	15	0.500	0.110	69,420	3,662	6,716,452
458–549	250–300	43	3.338	0.399	66,920	23,567	54,580,681
549–640	300–350	42	2.823	0.168	75,250	22,409	41,983,921
640–732	350–400	19	2.795	0.653	84,790	25,004	91,353,003
732–824	400–450	1	0.300	0.079	88,970	2,815	7,443,949
824–915	450–500	0	0.000	0.000	99,370	0	0
Totals		120			484,730	77,457	202,078,006

able biomass of *H. laevigatus* than does Niihau. In aggregate, we estimate the exploitable stock at all islands to be $B_{\Sigma tot} = 271.4\,MT$ ($p[217.3 \leqslant B_{\Sigma tot} \leqslant 325.5] = 0.95$, SE 27.6 MT, CV 10.18%).

Analysis of length-frequency data

Although the Kaulakahi Channel study site was sampled on seven different occasions over a 29-month period

(May 1986–October 1988), during which over 6800 female and 11,800 male shrimp were sexed and measured, there was little evidence of progression in size modes (Fig. 7). The CL frequency distributions of male shrimp were particularly stagnant, and those of females showed no coherent pattern that could be attributed to the influx of year-classes into the exploitable population.

Due to the apparent stationary behavior of these

Figure 7
Length-frequency distributions of female and male *Heterocarpus laevigatus* at the Kaulakahi Channel study site.

Figure 8
Composite length-frequency distributions for all female and male *Heterocarpus laevigatus* sampled.

Figure 9
Yield-per-recruit of *Heterocarpus laevigatus* and estimates of optimum exploitation level ($F_{0.1}/M$).

distributions, all the length data were pooled (Fig. 8). It is evident from the figure that female shrimp reach substantially larger sizes than do males, in agreement with previously published work (Dailey and Ralston 1986, Moffitt and Polovina 1987). Superimposed on the combined length-frequency distributions of males and females is the estimated size of *H. laevigatus* when fully vulnerable to the traps (i.e., $CL_{co} = 30 \text{ mm CL}$). The carapace width of shrimp this size is equal to 1.27 cm (0.5″), the minimum mesh size of the traps.

We applied the Wetherall et al. (1987) regression method to these length-frequency data and estimated that $\Theta_\varphi = 1.01 \pm 0.052$ and $\Theta_\sigma = 0.74 \pm 0.075$. For females we estimated that $CL_\infty = 58 \text{ mm}$ (SE 0.37) and for males $CL_\infty = 50 \text{ mm}$ (SE 0.44), corresponding to $W_\infty = 80 \text{ g}$ for females and 55 g for males.
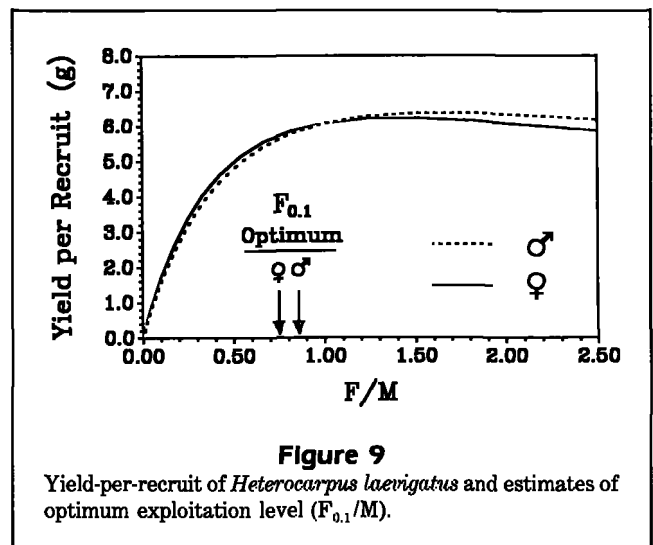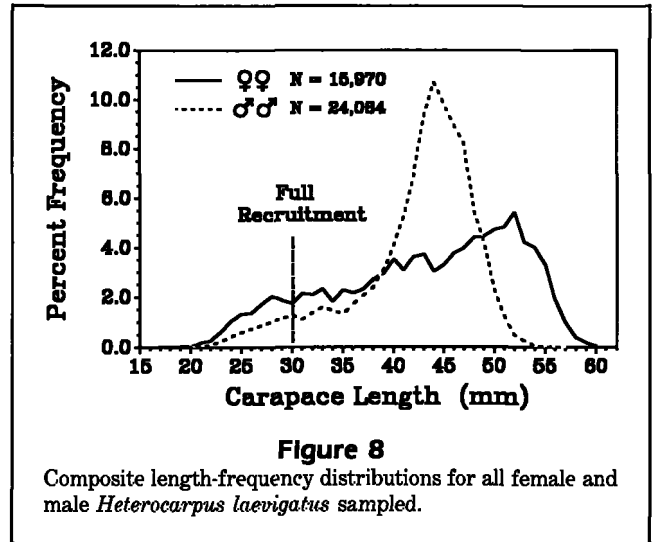
The smallest shrimp we captured in the pyramid traps was 16 mm CL. Below this size, selectivity of the gear was zero. By equating carapace width and mesh size, we determined that $CL_{co} = 30 \text{ mm}$. Thus, our estimate of the size at 50% recruitment to the fishery ($CL_{r'}$) is 23 mm. Given this result, and sex-specific estimates of Θ and W_∞, we calculate that for females $F_{0.1}/M = 0.75$ and for males $F_{0.1}/M = 0.86$ (Fig. 9).

Discussion

In this assessment, projections of exploitable biomass depend greatly on the estimate of catchability obtained from the Leslie depletion experiment. Due to its major role in the calculations, sources of bias in its estimation must be considered carefully.

There is evidence to show that estimates of crustacean population size obtained through survey removal methods like the Leslie and DeLury methods (Ricker 1975) may severely misrepresent the actual size of the population. In his study, Morrissy (1975) found that DeLury estimates of population number of *Cherax tenuimanus* were anywhere from 39 to 53% of those based on a complete count of the population. Similarly, DeLury estimates of the population density of *Panulirus cygnus* were 25% of those estimated from diver counts (Morgan 1974a).

The most likely origin of bias in these situations is that not all individuals in the exploitable portion of the population are equally vulnerable (*sensu* Morrissy 1973) to the gear. For example, when sampling with baited drop nets, the catch of *C. tenuimanus* in intermolt, expressed as a known fraction of the actual population, was much higher than the catch in a premolt condition; individuals in molt stages immediately preceding and following ecdysis were not caught at all (Morrissy 1975).

It is possible that a similar bias was operating during the depletion study at the Kaulakahi Channel study site. The presence of shrimp in the exploitable portion of the population, which were less susceptible to trapping, would result in overestimation of catchability and underestimation of biomass. Factors such as molt stage (Morgan 1974b, Morrissy 1975), sex (Morrissy 1973), and feeding history (Sainte-Marie 1987) are known to cause variation in vulnerability to trapping. Although social dominance, mediated through differences in size, can affect catchability (Morrissy 1973, Chittleborough 1974), it is unlikely to have substantially biased our results because the catch size-structure remained unchanged during the experiment (Fig. 3). Also, Gooding et al. (1988) did not see "any overt aggressive behavior" among *H. ensifer* that were active around baits. Lastly, seasonal and interannual alterations in catchability due to temperature (Chittleborough 1970, Morgan 1974b), salinity (Morgan 1974b), and food availability (Chittleborough 1970) operate over longer time-scales than the depletion experiment.

Two other lines of evidence support the premise that shrimp biomass was underestimated. Although results presented in Figure 4 indicate that 12 days of trapping dropped the catch rate to 48% of its starting value (10.87 kg/trap-night), it had risen to 19.73 kg/trap-night when resampled 47 days later (data from 9–11 July 1986 cruise; see Table 1). If catchability is estimated from the decline in catch rate that occurred between the beginning of the depletion study (22.84 kg/trap-night) to the time the site was resampled 2 months later, and we assume the decline was due only to trap removals (1499.00 kg), we obtain $\hat{q}=2.4624$ ha/trap-night. This represents a 74% reduction in the estimate,

which in turn would inflate biomass estimates by a factor of 3.85 (i.e., $B_{\Sigma tot} = 1050$ MT). This relative bias is similar to that reported by Morgan (1974a) for *Panulirus cygnus* (see above).

From submersible observations of *H. laevigatus* density, Moffitt and Parrish (1992) obtained $\hat{q}=0.2895$ ha/trap-night for the same traps we used, amounting to a 33-fold difference relative to our Leslie analysis. They, too, expressed concerns about bias in catchability estimates derived from depletion experiments due to variable susceptibility to the gear. Conversely, their estimate of catchability was based on comparing site-specific March 1988 trap catches with submersible observations made during August, even though *H. laevigatus* undergoes seasonal vertical migrations (King 1983, Dailey and Ralston 1986). In addition, at the start of each dive, they deployed a baited trap in the area of the submersible. Both factors could lead to underestimation of catchability.

It is clear that biased estimates of q will result if the probability of capture is not uniform among shrimp. In an attempt to solve this problem, Quinn (1987) developed a depletion model that explicitly incorporated a term for non-constant catchability. Application of his model to Pacific halibut effectively accounted for short-term trends in q, but auxiliary estimates of fishing and natural mortality were required, data that are unavailable here.

The primary objective of this study was to determine the exploitable biomass of *H. laevigatus* in the main Hawaiian Is. (MHI). Even if shrimp biomass were as high 1050 MT, rather than 271 MT (see above), our results indicate that the MHI stock is much smaller than previously believed, and that prior estimates of maximum sustainable yield (MSY) are much too high. For example, Struhsaker and Aasted (1974), using figures from a fishery for *H. reedi* off the coast of Chile, speculated that *H. ensifer* in Hawaii could sustain a level of production equal to 10–20 kg/ha·yr^{-1}. If *H. laevigatus* were assumed to be equally productive (e.g., Anon. 1979), then, given there are ~350,000 ha of prime habitat at 458–640 m (250–350 fm) in the MHI alone (Table 2), the resulting estimate of MSY exceeds stock biomass many times over. Moreover, catch rates of *H. laevigatus* in the distant Northwestern Hawaiian Is. (Nihoa to Kure), which represent a similar amount of shrimp habitat as the MHI, are no more than half those observed in the MHI (Gooding 1984, Tagami and Barrows 1988, Tagami and Ralston 1988).

Our estimates of $\Theta_Q = 1.01$ and $\Theta_\sigma = 0.74$ are much lower than those given in Dailey and Ralston (1986), who reported $\Theta_Q = 2.9$ and $\Theta_\sigma = 4.3$. By requiring CL_{∞} to be greater than the modal size, they effectively constrained Θ to values much greater than unity. A similar requirement was imposed by Moffitt and Polovina

(1987), who estimated $\Theta_Q = 1.9$ and $\Theta_\sigma = 2.1$ for *H. lae-vigatus* in the Mariana Is. Additionally, use of the "mode" criterion to establish the minimum size at full vulnerability results in substantially greater sensitivity of Θ to input estimates of CL_{co}. For example, if CL_{co} is 30 mm as we suggest (Fig. 8), ± 2 mm perturbations in CL_{co} result in -9% and $+12\%$ changes in estimates of Θ_σ. However, if the mode of the size-frequency distribution is used instead ($CL_{co} = 44$ mm), the same perturbations alter estimates of Θ_σ by -16% and $+46\%$. Similar sensitivity was observed in estimates of Θ_Q. In summary, it is our belief that independent estimates of CL_{co} are superior to those obtained from the size data analyzed, particularly when there is no reason to suspect that agonistic interactions affect the catch size-structure.

Lower values of Θ indicate a reduction in the instantaneous mortality rate (Z), an increase in the von Bertalanffy growth coefficient (K), or both. We favor the first hypothesis, largely because of the cold (4–6°C), trophically-impoverished habitat in which *H. laevigatus* reside. In many respects these shrimp represent a crustacean analog to Pacific ocean perch *Sebastes alutus*, which grow very slowly, exhibit extreme longevity, and display low rates of natural mortality (Leaman and Beamish 1984). Consequences of this life-history pattern are that (1) under pristine conditions, individuals accumulate in the largest size-categories (Fig. 8), (2) the ratio of production to biomass is low, and (3) stocks are very susceptible to overfishing.

Acknowledgments

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