

Abstract. – Five submersible dives were conducted to evaluate the behavior of deepwater shrimp and the relationship of their density to bottom type and trap yield. Differences in behavior of two species of *Heterocarpus* were observed: *H. ensifer* tended to group around large anemones and other benthic relief over otherwise flat, sandy bottom and were very active in the presence of a baited container; whereas *H. laevigatus* were solitary and showed little activity around a baited container. Greater densities of *H. laevigatus* were observed on volcanic than on coralline substrate, indicating a possible association with this bottom type. Trap catches were regressed against observed *H. laevigatus* densities yielding an estimate of the catchability coefficient. This coefficient differed from that obtained from a previously conducted Leslie model depletion study. Factors contributing to this difference may include comparing estimates of catchability based on data from different areas, bias in the estimate of catchability based on observed density, and bias in the estimate of catchability from the depletion study. A combined fishing and visual census study is suggested as the best assessment technique.

An assessment of the exploitable biomass of *Heterocarpus laevigatus* in the main Hawaiian Islands.

Part 2: Observations from a submersible

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Tropical deepwater pandalid shrimp have potential for commercial harvesting in many areas of the Pacific (Struhsaker and Aasted 1974, Wilder 1977, Moffitt 1983, King 1984, Tagami and Barrows 1988). These shrimp are readily trapped but not easily trawled (Struhsaker and Aasted 1974). The largest and most commercially desirable species in Hawaii is *Heterocarpus laevigatus* (Tagami and Barrows 1988); the smaller *H. ensifer* has less commercial appeal but is also abundant (Struhsaker and Aasted 1974). In the early 1980s, several boats initiated a trap fishery targeting *H. laevigatus*, and landings rose to a high of 159 metric tons (t) in 1984 (HDLNR 1986). By 1985, most vessels left the fishery, and the annual landings dropped to <6t/yr (West. Pac. Fish. Inf. Network, NMFS Honolulu Lab., unpubl. data).

Early predictions of maximum sustainable yield for Hawaiian shrimp, based on little or no direct data, were as much as 1000–2000t/yr (Struhsaker and Aasted 1974, HDLNR 1979). Recent research on population dynamics combined with systematic trapping surveys has resulted in more refined estimates of exploitable biomass and maximum sustainable yield for *H. laevigatus* in various island locations (Dailey and Ralston 1986, Ralston 1986, Moffitt and Polo-

vina 1987, Ralston and Tagami 1992). The most recent estimate of exploitable biomass for the main Hawaiian Islands, 271–1050t, is based on an estimate of the catchability coefficient (q) obtained through a Leslie model depletion study, coupled with catch-per-unit-effort (CPUE) values and habitat area estimates obtained through systematic trapping (Ralston and Tagami 1992).

The relationship of observed target-species density to fishing-gear CPUE has been used to estimate stock biomass and catchability (Ralston et al. 1986, Kulbicki 1988). Estimates of abundance obtained through visual census techniques are generally higher than those based on catches of fishing gear, and the relative reliability of the various assessment methods must be analyzed on a case-by-case basis (Uzmann et al. 1977, Powles and Barans 1980, Kulbicki and Wantiez 1990, Matlock et al. 1991).

In the present study, we conducted submersible dives at several sites in the Hawaiian Islands to observe shrimp behavior both away from and in the vicinity of a baited container and to record density and substrate associations of *H. laevigatus*. Observations of shrimp behavior and substrate associations have applications to commercial fishermen in terms of

trapping technique and site selection. The mean of observed densities recorded during submersible dives is regressed against yields of a trap set at the dive sites to obtain an estimate of q , and this value is compared with that reported by Ralston and Tagami (1992). An accurate estimate of catchability is important in order to better estimate exploitable biomass for management purposes.

Methods

A total of five submersible dives were conducted in the main Hawaiian Islands, at two sites off leeward Oahu in February 1988 and three sites off the Kona coast of the Island of Hawaii in August 1988 (Table 1). The Oahu sites were selected for their proximity to port and because of previously-observed concentrations in the area of unidentified red shrimp at appropriate depths (400–900 m) for *Heterocarpus*. The three Kona sites were selected as extremes in *H. laevigatus* yield for the area during a trapping survey using pyramid traps conducted in March 1988 (see Tagami and Barrows (1988) and Ralston and Tagami (1992) for trap description and trapping methods). Catches of *H. laevigatus* were lowest for the Kona area (<1 kg/trap-night) at one of the sites and highest (>10 kg/trap-night) at the remaining two sites.

Visual censuses

All dives used the *Pisces V*, a three-man submersible that allowed simultaneous observations by two researchers through separate view ports with non-overlapping fields of view directed diagonally forward and down. A video camera continuously recorded the bottom throughout each dive as well. The same two researchers estimated shrimp abundance on all dives and independently reviewed the dive video tapes as a check on observer bias. On each survey, the submersible descended to depths of 480–920 m, then traveled to an arbitrary starting location at ~600–750 m depth. At this point, a baited container was placed on the bottom and observations of shrimp behavior in the presence of bait were recorded. After observing shrimp behavior for ~15 min, the submersible traveled a haphazard, rectangular track at a speed of ~2 knots along the contours within the zone of maximum shrimp abundance (defined below), returning to the baited container for retrieval at the end of the dive. At preselected time-intervals (5 or 10 min), the submersible settled to the bottom and counts of shrimp were taken by each observer in an independent quadrant filling the field of view. The estimated area of each quadrant was 10 m², which was calibrated by underwater observa-

Table 1
Locations of five study sites off the islands of Oahu and Hawaii and 1988 sampling dates.

Site no.	Location	Dive date	Trap date
Oahu			
1	21°19.3'N, 158°10.1'W	8 Feb.	13 Mar.
2	21°31.0'N, 158°16.8'W	9 Feb.	13 Mar.
Kona			
1	19°14.0'N, 155°54.9'W	23 Aug.	18 Mar.
2	19°20.7'N, 155°54.2'W	24 Aug.	18 Mar.
3	19°47.5'N, 156°07.8'W	25 Aug.	15 Mar.

tion of known dimensions with the submersible attached to its launch-and-retrieval vehicle. The minimum distance between observation sites was ~100 m. The number of observations of shrimp density varied between dives, for bottom time was dependent on battery power.

Bottom depth, temperature, and substrate type were recorded with each shrimp count. The substrate within each quadrant was categorized by composition and particle size of the major component. Substrate composition included coralline, volcanic, and mixed; particle size included sand, rock both small (~<15 cm diameter) and large (>15 cm diameter), and pavement.

A χ^2 goodness-of-fit test using a Poisson distribution for the expected frequencies was conducted to determine whether *H. laevigatus* were concentrated or evenly distributed over the bottom at each dive site. Mean *H. laevigatus* density and 95% CI was calculated for each dive site based on a Poisson distribution,

$$CL = D_{(i)} \pm (1.96) \left(\frac{D_{(i)}}{n_{(i)}} \right)^{1/2},$$

where $D_{(i)}$ and $n_{(i)}$ are the mean density and number of observations for each dive site. Expected density values (De) for each site were calculated using trap landings for the site and the normalized catchability coefficient (q) reported by Ralston and Tagami (1992), using the following formula:

$$De_{(i)} = \frac{CPUE_{(i)}}{q}.$$

Confidence limits for the expected density values for each site could not be calculated, since variance cannot be computed for CPUE, based as it is on the catch of a single trap.

An analysis of variance (ANOVA) was performed to determine whether higher mean densities of *H. laevi-*

gatus could be attributed to different dive sites or bottom types and to determine whether there was observer bias. Independent variables for the ANOVA were dive site, substrate material, substrate particle size, and observer.

Comparisons of trap landings and density estimates

Trap catch rates were obtained in March 1988 from one pyramid shrimp trap set at each of the five dive sites and allowed to soak overnight (see Ralston and Tagami (1992) for details). Trap catches of *H. laevigatus* were regressed against mean densities obtained from visual counts for the five study sites, fitting a linear model with a zero intercept. The slope of this regression is an estimate of q , which was compared with that reported by Ralston and Tagami (1992).

Results

A total of 923 shrimp were captured in the 5 pyramid traps set at the study sites. Of these, 705 (76%) were *H. laevigatus* (Table 2), 217 were *H. ensifer*, and 1 was *Acantheephyra eximia*. During the scheduled observation periods on the submersible dives, a total of 494 shrimp were observed (194 total quadrant observations). Of these, only 95 (19%) were *H. laevigatus*, and the remainder consisted primarily of *Plesionika* sp., tentatively identified as *P. ensis*, and a few individuals of *P. alcocki*, *H. ensifer*, *A. eximia*, and *Gnathophausia longispina*. All *H. laevigatus* observed from the submersible appeared well within the size range of those captured in the traps, indicating that both stock assessment methods sample the same population.

Visual censuses

During our dives, the shrimp showed little reaction to the presence of the submersible or its lights. When the submersible came within a few inches of the shrimp, they swam a short distance avoiding collision. When the photoflash was used, the shrimp within a few feet of the submersible started, darting a distance of 1–4 cm. No other reactions to the submersible or its lights were observed. Several behavioral differences were noted between the various species observed.

A total of 94% (89 of 95) of the *H. laevigatus* observed during census periods were seen between 550 and 675 m, the depth range herein defined as the zone of maximum abundance. Individuals of *H. laevigatus* were observed at each dive site, but not necessarily during the scheduled census periods conducted within the zone of maximum abundance. Only counts taken within

Table 2

Trap catches, predicted densities, and mean observed densities with 95% CL of *Heterocarpus laevigatus* at five study sites off the islands of Oahu and Hawaii in 1988. N = the number of observations.

Dive site	Trap catch (n/trap)	Density (n/ha)		CL	N
		Predicted	Observed		
Oahu					
1	5	0.53	0	—	34
2	26	2.7	0	—	8
Kona					
1	0	0	200	(-680)-1080	10
2	376	40	1360	(-570)-3290	14
3	298	31	890	220-1560	76

this depth range were used in the analysis.

Heterocarpus laevigatus were observed as solitary individuals on the bottom, usually stationary but occasionally walking, and rarely swimming near the bottom. They showed little activity in the presence of a baited container and were not observed crawling over or entering it. Conversely, *H. ensifer* were found in groups near relief features (e.g., large sea anemones) at shallower (450–550 m) depths, either stationary on the bottom or swimming about 1 m above the bottom. They were very active in the presence of a baited container, aggregating quickly and crawling over and entering the container through the mesh and other holes. *Plesionika alcocki* usually were seen on the bottom, whereas *P. ensis* generally were seen hanging motionless in the water column ~1–2 m off the bottom. Each showed some activity around the baited container. *Acantheephyra eximia* and *G. longispina* were observed swimming 1–2 m off the bottom, but were not seen at the baited container.

Bottom temperature varied during the dives from a low of 3.9°C at 920 m to a high of 6.0°C at 480 m. The temperature range within the zone of maximum *H. laevigatus* abundance was 4.8–5.9°C.

Bottom type varied considerably among the sites. The bottom at the two Oahu sites was classified as coralline sand making up an even, featureless plain with a gradual (<20°) slope. The bottom at the three Kona coast sites was much steeper, generally about a 35–45° slope, but with some sections near vertical or even slightly undercut at the Kona site 3. At Kona site 1, the bottom was nearly uniformly composed of small (5–10 cm diameter), sharp-edged volcanic rocks and very little coralline material. Kona site 2 differed from site 1 in that the small volcanic rocks were more weathered and the substrate had a greater coralline component. Kona site 3 had many sandy areas, at

Table 3Analysis of variance for *Heterocarpus laevigatus* density by dive, bottom type, and observer.

Source	df	SS	MS	F	P
Dive	4	31.25	7.81	6.87	0.0001
Substrate material	2	24.53	12.26	10.79	0.0001
particle size	3	5.96	2.98	2.62	0.0765
Observer	1	3.40	3.40	2.99	0.0859
Error	132	150.08	1.14	—	—
Corrected total	141	215.22	—	—	—

times covering the entire 10 m² quadrant, as well as areas of exposed limestone often forming undercut cliffs, and areas of small weathered volcanic rocks.

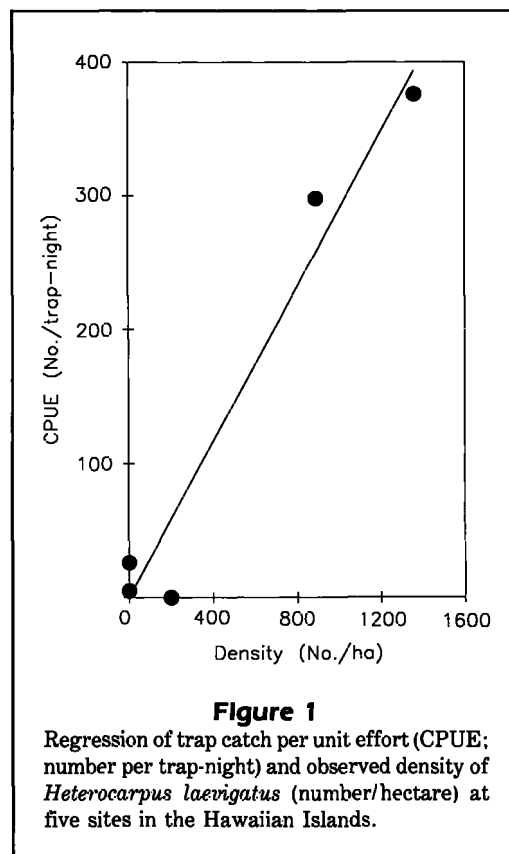
The distribution of *H. laevigatus* over the bottom was evaluated in several ways. No significant values were found for the χ^2 goodness-of-fit tests ($P > 0.10$) of the density observations recorded at each dive site, suggesting that the shrimp were randomly distributed (in a Poisson manner) instead of clumped at each dive site. The mean and confidence intervals of *H. laevigatus* density observed at each dive site are presented in Table 2. Pooling data from all dive sites for the independent variables (dive site, substrate material, substrate particle size, and observer), only dive site and substrate material were significantly correlated with shrimp density (ANOVA, $P < 0.05$; Table 3). The distribution of residuals did not differ significantly from a normal distribution. Independent review of the dive video by each observer yielded complete agreement on *H. laevigatus* counts and substrate classification, indicating a lack of observer bias in shrimp density estimation and substrate associations.

Comparisons of trap landings and density estimates

Mean observed densities were regressed on trap catches for each dive site (Fig. 1) ($r^2 = 0.97$, $P = 0.0003$). The least-squares regression equation is

$$\text{CPUE}_i = 0.2896 (D_i), \quad (\text{SE } 0.02364).$$

An estimate of catchability is obtained directly from the value of the slope (0.2896 ha/trap-night) with a confidence interval calculated as 0.2144–0.3648/trap-night. This estimate of catchability is $< \frac{1}{30}$ th that reported by Ralston and Tagami (1992) and is reflected in the differences between observed and

**Figure 1**

Regression of trap catch per unit effort (CPUE; number per trap-night) and observed density of *Heterocarpus laevigatus* (number/hectare) at five sites in the Hawaiian Islands.

expected *H. laevigatus* densities for Kona sites 2 and 3 (Table 2).

Discussion

Differences in behavior between *H. laevigatus* and *H. ensifer*, the two species with greatest commercial potential, may lead to some practical applications for fishermen. The high activity level noted for *H. ensifer* in the presence of a baited container has also been reported by Gooding et al. (1988) and Saunders and Hastie (1989). The rapid attraction and entry of this species into traps, even during daylight hours, indicate that a short soak time may be adequate for commercial harvesting. The lower activity level of *H. laevigatus* observed in our study and reported by Saunders and Hastie (1989) may indicate that a longer soak time is more appropriate for this species. If so, a small vessel with a limited number of traps could maximize total catch by making two short sets during daylight hours on *H. ensifer* grounds, followed by an overnight set on *H. laevigatus* grounds, assuming that suitable concentrations of both species are present within a reasonable proximity.

Previous observations of *H. ensifer* from a submersible found higher densities on flat, silty, sandy areas than over low-relief, rocky outcroppings (Gooding et al. 1988). Although statistical analysis of substrate associations were not conducted for *H. ensifer* in this study, we did observe a similar substrate association. *Heterocarpus ensifer* were abundant at the Oahu dive sites at depths (500–800 m), although this is deeper than their reported optimum range of 300–600 m (Gooding 1984). The substrate on these two dives was flat, coralline sand with few isolated, low-profile features (e.g., sea anemones, small rocks) around which the shrimp appeared to concentrate. No rocky outcroppings were observed on these dives. Very few *H. ensifer* were observed at the three Kona dive sites, where the bottom was steep and composed largely of rocky rubble with few sandy patches, though the dive depths again were deeper than the optimum range for this species.

The substrate associations of *H. laevigatus* appeared to differ from those of *H. ensifer*. Although the differences in substrate particle size were not significant, the ANOVA test revealed significantly higher densities on volcanic compared with coralline substrates (Table 3) with data from all dive sites pooled. The significant results for substrate type, however, must be viewed with caution because of the significance of dive site to *H. laevigatus* density and the unbalanced sample design. Not only were all substrate types not present on a single dive, but those types present were not found in equal proportions on any dive. Therefore, differences in density attributed to substrate type may actually be a reflection of differences related by some other factor to dive site. In particular, the Kona dive sites were largely volcanic, and the majority of the *H. laevigatus* observed were from Kona sites 2 and 3. Although Kona site 1 also was largely volcanic, the volcanic rocks differed from those observed at sites 2 and 3, in that the appearance was of a more recent rock slide (sharper edges vs. weathered). This apparent instability may be responsible for the low shrimp density observed at site 1. Other aspects of the bottom, such as slope, substrate complexity, stability, and current patterns may be of considerable importance and should be investigated in future work on the substrate associations of *H. laevigatus*.

With visual censusing techniques, there is always a concern regarding the reliability of abundance estimates. Various factors, including sampling techniques, species behavior, and physical conditions, can bias results (Colton and Alevizon 1981, Sale and Douglas 1981, Brock 1982, Ralston et al. 1986, Matlock et al. 1991). Some authors believe that density estimates based on direct visual surveys, though often much higher, are more reliable than those estimated from fishing gear catches (Uzmann et al. 1977, Powles and

Barans 1980, Kulbicki and Wantiez 1990). Individuals of the target species, *H. laevigatus*, were easily counted because they were in the open and reacted almost with indifference to the presence of the submersible, and because the low, uncomplicated relief at the study sites offered little opportunity for their concealment. Avoidance of the submersible by the shrimp seems unlikely. Observed densities were much greater than expected, yet these would be underestimates if avoidance occurred. We cannot discount the possibility of bias in our density estimates caused by attraction of shrimp to the baited container placed at the beginning of our dives. However, we observed no increased density gradient in the vicinity of the container, and density observations were taken well away from the container site (>100 m), presumably outside the drawing range of the bait, leading us to believe that bias due to this source was small.

Recalculation of exploitable biomass for the main Hawaiian Islands using Ralston and Tagami (1992) data and methods, but substituting the q value obtained in this study, would lead to a 33-fold increase in the estimate of exploitable biomass (~9000 t instead of 271 t). Just as Ralston and Tagami (1992) suggest that their estimate may be too low, we suggest that 9000 t may be unreasonably high, considering the preliminary nature of this estimate and the failure of the Hawaiian fishery that was at least partly due to drops in catch rates at annual yields of <200 t (Tagami and Barrows 1988). The acceptance of either of these estimates would drastically affect management decisions, and careful evaluation of these two values must be made. Contributions to the difference between the two estimates may be from three sources: actual differences in catchability for the two studies related to differences in time and study locations, error in our estimate of q , and error in the Ralston and Tagami (1992) estimate.

The estimation of q can be influenced by a variety of factors including currents, water turbidity and temperature, type of bait, soak time of fishing gear, and density of the target species (Morgan 1974, Richards and Schnute 1986, Miller 1990). For the two studies involved in this discussion, many of the potential sources of error were standardized. Both studies used the same traps, same bait, and same soak times. They did not, however, conduct studies at the same location or time, and the range of catch rates encountered differed for the two studies. In both studies it is assumed that catchability is constant for all catch rates and densities involved, but this may not be true, particularly between studies. Unfortunately, we are unable to evaluate the extent of the error involved from these sources.

The estimate of q presented in this study could also be biased. Sources of potential bias include lack of

representative catch rates for study sites, error in density estimation, incompatibility of CPUE and density estimates collected at different points in time, and the few data pairs involved. Not only were shrimp catches for each dive site based on a single trap-night of effort, but also traps generally were set at depths greater than the observed range of maximum abundance determined from our submersible observations (~750 m vs. 550–675 m). This results in no estimate of error for CPUE estimates at each site and no way to determine whether the traps were set within the range of maximum shrimp abundance at the time of trapping. If the traps were not set within this zone, yields at our sites may underrepresent relative shrimp abundance, leading to a lower-than-actual estimate of q . Another potential source of error in our q estimate is the accuracy of our density estimate. Confidence limits on our density estimates are quite broad, allowing for a fair degree of error. At many dive sites this problem is related to the few observations of density taken within the zone of maximum abundance. Additional problems in density estimation associated with the presence of bait in the water during the dives have already been addressed. The question of compatibility between data pairs of density estimates and CPUE values obtained at different points in time stems from possible changes in density or in q over time. Although trap catch rates in the Mariana Archipelago did not vary significantly on a seasonal basis (Polovina et al. 1985), suggesting that q does not vary seasonally, *H. laevigatus* may undergo temporal changes in depth range on either a diurnal or seasonal basis (King 1984, Dailey and Ralston 1986). If such movements do occur (the evidence is not strong) and depth range expands or contracts during these changes, densities observed during midday periods in February and August may differ from those occurring during trapping in March. Finally, although the fit is quite good, our estimate of q is based on only five data pairs covering limited values of CPUE and density.

The potential error in the Ralston and Tagami (1992) q estimate depends on the appropriateness of using their habitat area estimate in normalizing q and the validity of the assumption of constant catchability for all members of the population. These error sources are not necessarily greater than those discussed above, but are much easier to quantify. Even when an accurate estimate of biomass is obtained for a study site, calculation of a normalized q is dependent on the estimated habitat area of the study site. Estimated habitat area is apt to be larger when depth range is estimated from trap catches, as opposed to visual surveys, because of the ability of the traps to draw shrimp outside of their normal depth range. Recalculating the habitat area of the Ralston and Tagami study site using the observed

depth range (550–675 m) instead of the reported range (420–640 m) results in a reduction in area to 63% of the original value (748 ha instead of 1187 ha). Normalizing q with this reduced study-site area estimate gives an adjusted q value of 5.999 ha/trap-night (CI 2.6709–9.3271 ha/trap-night). The ratio of this adjusted value to the q obtained in the present study is 20.7 instead of the original 32.7. Ralston and Tagami (1992) discuss the effect on their q value of a large portion of the population not being susceptible to trap capture for the duration of the study period. They supply evidence that their original estimate of catchability may have been four times too high, resulting in a four-fold underestimation of exploitable biomass. Other authors have reported similar overestimates of catchability resulting from depletion studies (Morgan 1974, Morrissey 1975, Miller 1990). A further four-fold reduction of the Ralston and Tagami q value results in a ratio of 5.9 relative to our q value and only 1.8 for the extremes of the 95% CL (the minimum value for the Ralston and Tagami confidence interval compared with our maximum value). Coupling these quantifiable factors with the non-quantifiable factors discussed above could bring the two estimates of catchability into agreement.

Because of the importance of accurate estimates of exploitable biomass to the management process, it would be desirable to conduct a combined technique survey of the *H. laevigatus* resource. This should include direct visual density estimation with a trapping study conducted at the same time and place to obtain a reliable estimate of catchability and thereby exploitable biomass. Until that time, the expanded exploitable biomass estimate (1050 t) for the main Hawaiian Islands as presented by Ralston and Tagami (1992) should be accepted for management purposes as a reasonable, conservative approximation.

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