Abstract.-Densities of juveniles of the Hawaiian deepwater snapper *Pristipomoides filamentosus* were surveyed for 3 years in relation to their demersal environment at an east Oahu study site. Juveniles settled annually to spatially stable aggregations, occupying expanses of uniform sedimentary habitat. Habitat data were collected and used in a logistic regression model to predict correctly 68% of the juveniles' spatial variability. Premium habitat was identified as a sediment bottom, free of relief, and close to focused sources of drainage (reef platforms, embayments, and anthropogenic sources) in adjacent shallows. Surveys for juveniles elsewhere on insular slopes of the Hawaiian Archipelago indicated low juvenile abundance except at infrequent locations close to point sources of coastal drainage. Estimates of recruit production, based on densities of juveniles from other than premium habitat, were a small fraction of the recruits needed (calculated from catch) to account for the fishery's current landings of adult snappers. The 68-fold higher juvenile abundance at premium habitat can reconcile this difference, indicating that such infrequent high-quality habitat is an important (perhaps critical) fishery resource.

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Nursery habitat in relation to production of juvenile pink snapper, *Pristipomoides filamentosus*, in the Hawaiian Archipelago

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Understanding favorable nursery habitat and its contribution to the standing stock of adults provides an important perspective for managing demersal fisheries. In the tropics, such nursery habitat has been studied effectively for many species inhabiting shallower depths (Bardach, 1959; Parrish, 1989; Birkeland[1]). Species using deeper, more remote nursery grounds have received less attention, and as a result, habitat often is not considered adequately in fishery modelling or management planning. In places with limited demersal nursery habitat, such as the minimal shelf area of oceanic islands, this habitat may represent a resource of critical importance to the fishery. Accelerated coastal development on many islands could degrade unrecognized favorable nursery habitat and impact fishery resources. This paper examines the nursery habitat of the deepwater Hawaiian pink snapper, *Pristipomoides filamentosus*, in relation to the spatial variability of its juveniles. A study site at a productive nursery ground was intensively surveyed, and the results compared with surveys made over much of the archipelago. The implications of the variable habitat quality for the stock of adult snappers inhabiting the archipelago were then considered.

The pink snapper accounts for more than 40% of the State of Hawaii's $3 million annual commercial bottomfish catch[2] and is well represented in the extensive recreational catch. However, study and management of the adult stock has been historically difficult because of its patchy distribution and poorly recorded recreational landings (Ralston and Polovina, 1982). A productive research approach may be to study the juveniles of the species, which are free of fishing pressure and of the factors that affect recruitment to the adult population. Recent discovery (F. A. Parrish, 1989) of a dense, stable aggregation of juveniles in a nursery area has made this approach feasible. Juveniles (7–25 cm fork length [FL]) occupy moderate depths (60–90 m) in patchy aggregations on the insular shelf for less than a year before moving deeper (150–190 m) as they mature

[1] Birkeland, C. 1985. Ecological interactions between mangroves, seagrass beds, and coral reefs. United Nations Environmental Program Regional Series Report and Studies 73, 126 p.

[2] WPRFMC (Western Pacific Regional Fishery Management Council). 1993. Bottomfish and seamount groundfish fisheries of the Western Pacific region. NOAA NA17FC0062-02, Honolulu, HI, 57 p. WPRFMC, 1164 Bishop Street, Suite 1405, Honolulu, HI 96813.

(Moffitt and Parrish, 1996). Sonic tracks of these juveniles indicate a discrete and limited individual home range of 140 m average diameter, suggesting that the locations of these juvenile aggregations could be very stable. Why juvenile aggregations appear spatially stable and how common they are in the rest of the archipelago are the primary focus of this work.

Methods

Survey of the east Oahu study site

The east Oahu study site contains three submarine canyons. Two of the canyons are located just outside Kaneohe Bay, north of Mokapu Point, and the third is located south of Mokapu Point just outside Kailua Bay (Fig. 1, II). Throughout this paper, the three areas will be referred to as the "north Kaneohe," "south Kaneohe," and "Kailua" canyons. Positional data from a Global Positioning System (GPS) were entered and manipulated in a raster-based Geographic Information System (GIS)(IDRISI 4.0 version) (Eastman, 1992).

Video index of snapper abundance

A baited video camera (Fig. 2) was selected as the primary gear because it provided information on the abundance of snappers and their associated habitat type. In each video drop, the baited camera was placed on the bottom for 10 minutes, where it attracted juvenile snappers in front of the camera lens; the maximum number of snappers seen in a single image was used as the index of abundance. Consecutively deployed video drops were separated by 1,200 m to avoid attraction of fish from previous drops. A description of equipment, method, and validation of the technique for creating a video index of snapper abundance is provided by Ellis and DeMartini (1995).

Selected video stations at the study site were replicated to determine the suitability of unreplicated spatial data for subsequent use in evaluating the persistence of snapper patches over time. Nineteen stations, resampled after 10 days, were used to represent all 3 canyons during February–March 1994. These stations were termed "multicanyon stations."

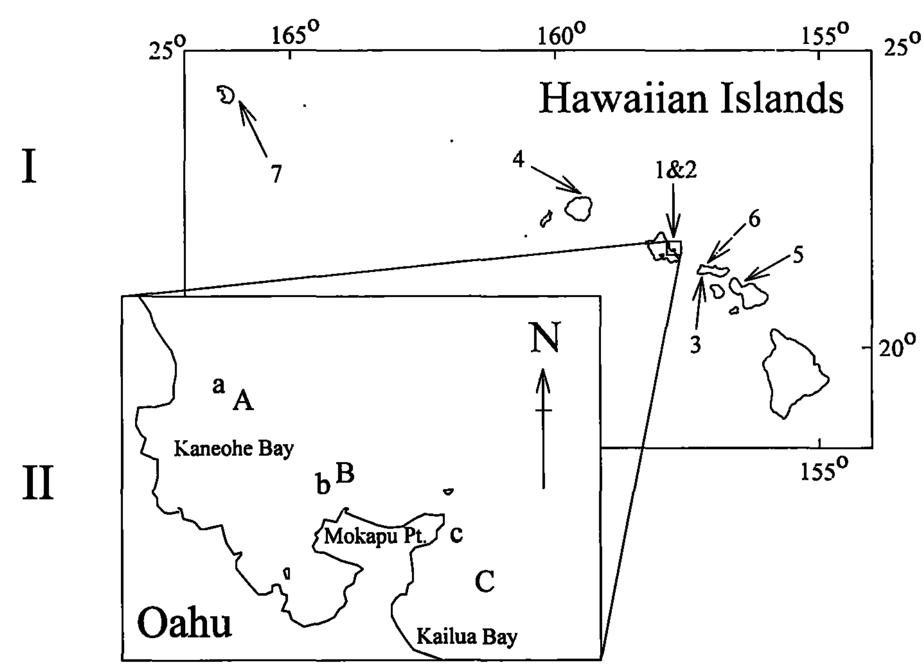

Figure 1

(I) - Map of the Hawaiian Archipelago with video survey sites denoted as 1 = Kailua-Oahu, 2 = Kaneohe-Oahu, 3 = south Molokai, 4 = Hanalei-Kauai, 5 = Kahului-Maui, 6 = north Molokai, and 7 = French Frigate Shoals in the Northwestern Hawaiian Islands. (II) Locations of the three east Oahu areas studied, including north Kaneohe canyon (A), south Kaneohe canyon (B), and Kailua canyon (C). Also represented are the sources of coastal drainage of north Kaneohe channel (a), south Kaneohe channel (b), and the Kailua wastewater outfall (c).

Interannual fidelity of snapper recruitment to the study site was assessed by using 20 video stations in the north Kaneohe canyon during 4 surveys in May 1992, May 1993, September 1993, and June 1994. These were designated as "multiyear stations" and were compared by using date of survey as a covariate.

Habitat characteristics

Slope, substrate type, sediment particle size, and proximity to closest known point sources of focused coastal drainage (channels through reefs and wastewater outfalls) were determined for all areas. The effect of slope on snapper abundance was assessed by using a GIS slope algorithm with collected bathymetry data. At the depths frequented by juvenile snappers, the habitat is typically dominated by a featureless expanse of sediment. To test the effect of alternative substrates on snapper abundance, types of substrate (as identified in video and chromoscope images) were coded as categories: e.g. soft sediments, escarpment-type relief (exposed edges of shelf, about 3 m high), and hard, even bottom. Video drops that recorded alternate substrate, or were within a snapper home range (Moffitt and Parrish, 1996) of such observations, were compared with video drops on soft sediment, presumably away from the influence of the other substrate. Substrate of adjacent shallower (30–60 m) and deeper (90–120 m) habitats, where juveniles have been historically absent (F.A. Parrish, 1989; Moffitt and Parrish, 1996), were surveyed with a longshore transect of 14 video drops in each of the 2 depth ranges.

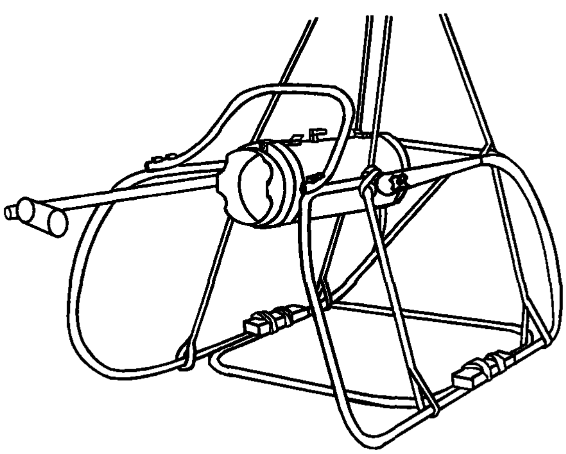

Figure 2

Diagram of the video camera system complete with bait canister mounted 60 cm in front of the lens. Source: Ellis and DeMartini (1995).

Ten bottom grab transects perpendicular to the bottom contours, each sampling 3 depths (45, 76, 106 m), were used to assess a possible relationship between snapper abundance and particle sizes in the sedimentary habitat. Replicate grabs were taken in line with and between the axes of the canyons in each area. Samples were wet-sieved into five size categories (>2.0, 0.35–2.0, 0.149–0.35, 0.0625–0.149, and <0.0625 mm).

The effect of some notable sources of natural and anthropogenic drainage present in each of the three canyons was considered. In Kaneohe, bay water drains through narrow channels (one in the north and one in the south, each with maximum depth of ~15 m at the seaward end) in the reef during ebb tide[3] (Fig. 1, II). In Kailua, increased suspended materials are introduced from an island wastewater and sewage outfall.[4] The video index of snapper abun-

[3] Bathen, K. H. 1968. A descriptive study of the physical oceanography of Kaneohe Bay. Oahu, Hawaii. HIMB Tech. Rep. 14, 353 p. Univ. Hawaii, 2550 The Mall, Honolulu, HI 96822.

[4] City and County of Honolulu. 1993–1994. Discharge monitoring reports. Environmental Protection Agency form 3320-1. Wastewater Division, 650 South King St. Honolulu, HI 96813.

Table 1

Depth, mean daily volume, and suspended load of the east Oahu drainage sources. The Kaneohe channels provide tidal drainage; the Kailua discharge is anthropogenic (24 hours).

Source of discharge	Discharge volume (m^3/day)	Discharge depth (m)	Suspended solids (kg/day)	Source
North Kaneohe channel	18.5×10^6	0–15	—	Bathen[1]
South Kaneohe channel	12.9×10^6	0–15	—	Bathen[1]
Kailua wastewater outfall	41,000	30	1,000	City and County of Honolulu[2]

[1]See Footnote 3 in the main body of the text.
[2]See Footnote 4 in the main body of the text.

dance was compared with the volume of each source's discharge (Table 1) divided by the distance separating the video samples from the nearest source of discharge. No attempt was made to sample the nutrients or suspended materials of these discharges. Elevated organics associated with these water masses are documented in the literature (Bromwell, 1992; City and County of Honolulu[4]; Laws and Allen[5]).

East Oahu statistical analysis

The distribution of the data and the categorical nature of the habitat variables required the use of nonparametric analysis (Siegel and Castellan, 1988). The type-I error for statistical significance was set at 0.05 (2-tailed test). Kruskal-Wallis ANOVA (K-W) was used to assess station effects in both "multicanyon and multiyear" analyses and to assess the effect of substrate type.

Differences in substrate by depth were tested with chi-square analysis. Replicate bottom grabs were compared by using Wilcoxon matched pairs sign ranks (MPSR), and Spearman's correlation was used for association of snappers with slope, sediment fractions, and influence of drainage.

Spatial variation of ranked snapper abundance was related to all habitat variables together by using logistic regression. Snapper abundance was grouped into two categories, aggregation present ($n \geq 5$) and aggregation absent ($n<5$), and assessed relative to the habitat variables that significantly influenced snapper abundance in the previously described univariate analyses (Norusis, 1992). Models of the variables and their plausible interaction effects were explored with the simple logistic regression model (Kleinbaum, 1992):

$$\pi = \frac{e^{\sum B_i X_i}}{1+e^{\sum B_i X_i}}, \qquad (1)$$

where π is the probability of detecting snappers with the linear combination of the habitat variables X_i in a given location. The coefficients estimated with the nonlinear regression by using maximum likelihood are represented by B_i. The base of the natural logarithm is e. The P-value for retention of independent variables in the model was set at 0.01.

[5] Laws, E. A., and C. B. Allen. 1993. Impact of land runoff on water quality in Kaneohe Bay, a subtropical Hawaiian estuary. Proceedings of the first biennial symposium for main Hawaiian islands marine resources investigation, November 17–18. Hawaii Department of Land and Natural Resource Technical Report 95-01, p. 232–248. Hawaii Dep. Land Natl. Resources, 1151 Punchbowl, Honolulu, HI 96813.

Survey of the archipelago

Conventional fishing gear (e.g. trawls, longlines, traps, handlines) was used to survey a total of 332 km of longshore habitat dispersed over seven islands of the archipelago (1989–94). The effectiveness of each gear at catching juvenile snappers was tested at the east Oahu study site. Sites surveyed included areas outside of embayments, places with large shelf areas at snapper depths, and sites of previous research fishing where juveniles had been documented incidentally (Struhsaker, 1973). Sites where snappers were found were then reassessed with longshore baited video surveys (range 5.5–42.6 km) to permit comparison with snapper abundance at the east Oahu study site. Numbers of juvenile snappers observed at each site were standardized by effort. The distance of each video drop from the coastal reef edge (15-m isobath) and the type of substrate seen in the video image were tabulated for each site; these variables were then compared with the respective video index of juvenile snapper abundance. Catch-per-unit-of-effort (CPUE) data from sets of conventional fishing gear at these coastlines were included to provide an independent index of snapper abundance.

In comparing video data from other coastlines with those of east Oahu, data for the two Kaneohe areas were pooled. Coastlines with point sources of drainage were identified, and the distance between sources of discharge and the video drops (weighted for maximum depth of discharge) were calculated. Importance of proximity to drainage sources to snapper abundance was then evaluated for these archipelago sites.

Snapper production estimates

To assess the importance of the contribution of juveniles from a site with premium habitat (e.g. Kaneohe) to the adult fishery, the adequacy of recruit production from other habitat areas was estimated. The density of snappers at habitat without snapper aggregations was compared with the density of snappers needed to explain the catch from the main Hawaiian Islands (MHI) commercial snapper fishery. Derived from mandatory reporting from the commercial fishery, the estimate is based on the catch of ~3-year-old snappers (termed "immature") just entering the MHI adult snapper fishery (Ralston, 1981; DeMartini et al., 1994). Based on the years 1989–92, the estimated mean annual catch, C (i.e. the commercial catch [WPRFMC[2]]) was ~22,000 immature (1.3 kg) snapper/year. Recreational fishing produces a significant additional catch in Hawaii, but it is poorly documented and was not considered in this estimate.

By using the estimated growth coefficient, k, of 0.25/yr derived for juvenile snappers (DeMartini et al., 1994) in the mortality relationship of $M/k \approx 2$ (Ralston, 1987a), the instantaneous natural mortality coefficient, M, was estimated as 0.50/yr, and a range for the instantaneous fishing mortality coefficient, F, was calculated. The low end of the range assumes $M = F$, on the basis of the fishery operating at maximum sustainable yield (Ralston and Polovina, 1982), providing an instantaneous F of 0.50/yr. The high end of the range assumes that fishing mortality is twice natural mortality, $F = 2M$ (Ralston, 1987b), resulting in an F of 1.0/yr. The two estimates of F were used independently to represent the extremes of the probable range. The mean standing stock of immature snappers, N_3, can be calculated by use of the conventional formula for the annual rate of exploitation (Everhart and Youngs, 1981; Gulland, 1983):

$$N_3 = \frac{C}{\frac{F}{F+M}\left(1-e^{-[F+M]}\right)}, \tag{2}$$

resulting in estimates of 42,500–69,600 fish. Because these immature snappers have been exposed to natural mortality for 2 years since the time t_1 that they inhabited nursery depths, a back calculation provides N_1, an initial estimate of juveniles supported on the MHI grounds. The formula (Gulland, 1983)

$$N_1 = \frac{N_3}{e^{-M(t_3-t_1)}}, \tag{3}$$

yielded values of N_1 between 115,600 and 189,200 fish. With this estimate of N_1, divided by the amount of bottom area in the MHI between the 60 and 90 m isobaths (2,600 km^2, NOS bathymetric charts), an estimate of the overall density of juvenile snappers required to support the current fishery was derived.

Results

The east Oahu study site

Two-hundred and eleven video camera drops with standard bait were dispersed throughout the insular slope (60–90 m depth) of the Oahu study site. Abundance data from the video drops were nonnormally distributed (33% zero observations) (Fig. 3). Snappers were found at each of the 3 east Oahu canyons. Snapper abundance differed significantly among the multicanyon stations (K-W, χ^2=35.6, P<0.01), confirming that relative spatial differences in snapper distribution remain stable (Fig. 4). In the multiyear stations at north Kaneohe canyon, essentially similar spatial differences persisted (K-W, χ^2=37.3, P<0.01); this finding suggests that successive years of juvenile snappers settle spatially according to habitat quality. Because the effect of station was significant for both the multicanyon and multiyear comparisons, the abundances of snappers at unreplicated video drops were considered representative of the habitat quality at those locations.

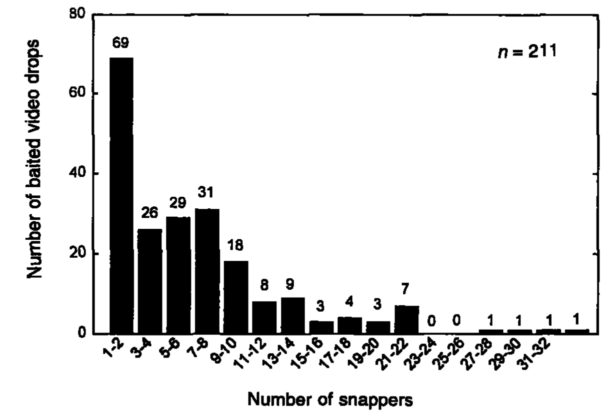

Figure 3

Distribution of occurrence of snappers in video drops at east Oahu sites.

Bottom slope was unrelated to the video indices of snapper abundance (Spearman's r_s=0.013, P=0.72). Substrate at 95% of the video drops (60–90 m) was composed of uniform, smooth sediment. High, escarpment-type relief was detected in only 3% of the drops. A significantly lower abundance of snappers occurred in the area surrounding escarpment-type relief than in the even sediment bottom (χ^2=11.48, P<0.001). The 95% confidence intervals of snapper densities at sites with relief (0–1 snappers) versus sites with sediment bottom (3–4 snappers) did not overlap. A similarly low abundance of snappers was associated with areas near exposed hard substrate (χ^2=10.50, P<0.01; 95% CI=0–2 snappers). Snapper grounds (60–90 m) and the adjacent deeper (90–120 m) area did not differ in the occurrence of soft sediment substrate (χ^2=0.44, P=0.43). However, the adjacent shallow grounds (30–60 m) had significantly more hard bottom and relief (χ^2=11.36, P<0.001); soft sediment occurred in fewer (71%) of the shallow video images.

The duplicate sediment grabs did not differ, suggesting that the sediment sampling effectively represented the soft bottom habitat (Wilcoxon MPSR, P=0.93). Of the 5 sediment fractions, snapper abun-

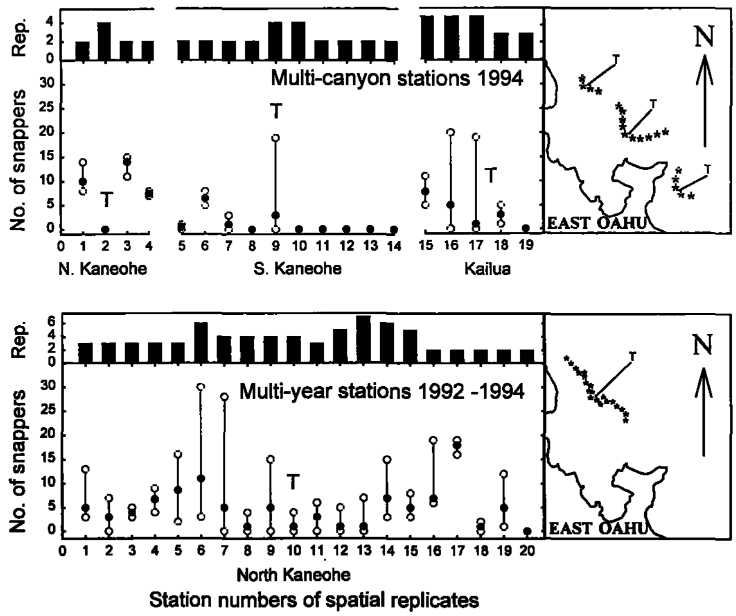

Figure 4

Mean (filled circle) and range (hollow circles) of east Oahu snapper station reliability test. The top graph is the 1994 multicanyon analysis and the bottom graph is the multiyear assessment (1992–94). The "T" on each graph represents the location of each canyon's axis or "trough." Numbers of replicates (Rep.) at each station are represented with bar graphs at the top of each graph. Maps on the right of each graph indicate the areas covered by the data.

dance was significantly correlated with only the clay-silt (<0.0625 mm) fraction (Spearman's r_s=0.35, P<0.001) (Table 2). The greatest abundance of clay-silt occurred in an area just northwest of the north Kaneohe canyon trough; at Kailua the abundance was less than half that at Kaneohe, and high concentrations spread southeast of the canyon trough.

Proximity of point sources of drainage was associated with snapper abundance, i.e. video index of snapper abundance and distance to discharge were significantly negatively correlated (r_s=–0.18, P<0.05). The weakness of the relationship resulted from the failure to consider the effect of bottom relief in the comparison. This result indicated the need for a model that considered the variables together.

Table 2

Spearman rank order correlation coefficients and probability values for snapper abundance with sediment particle size. In all comparisons sample size = 211.

Sediment size fraction (mm)	Correlation coefficient r_s	Probability value P
>2.000	–0.0426	0.54
0.350–2.000	–0.0932	0.178
0.149–0.350	–0.0922	0.184
0.063–0.149	0.0809	0.244
<0.063 (clay-silt)	0.3555	<0.001

Modeling of snapper aggregations.

The stepwise backward regression evaluated the relative importance of the 3 habitat variables found significant in the univariate analysis: 1) escarpment-type relief; 2) clay-silt (<0.0625 mm) sediment fraction; and 3) proximity of coastal discharge. The interaction of discharge with the presence of clay-silt was also assessed. All variables except clay-silt were retained by the model (P<0.01; Table 3). Reasons for the model's exclusion of clay-silt will be discussed later. The model correctly predicted overall presence (≥5) or absence (<5) of snapper aggregations for 68% of the video drops. The model predictions of presence (79% [≥5]) were roughly balanced by those for absence (60% [<5]) (Table 4). Ranked snapper abundance was interpolated by using all video drops to

Table 3

Statistical specifics associated with the regression for presence (≥5) or absence (<5), of snapper aggregations at east Oahu. Model chi-square (χ^2)=54.11, P<0.0001, df=3.

Name of variable	Estimated coefficient	Standard error	Probability value P
Cross product of clay-silt with proximity of drainage source	1.45×10^{-6}	3.47×10^{-7}	<0.0001
Distance to drainage	-7.5×10^{-7}	1.58×10^{-7}	<0.0001
Escarpment relief	–1.586	0.435	0.0003

provide an image of snapper distribution at east Oahu (Fig. 5).

Table 4

Two by two table of presence (≥5) or absence (<5) of snapper aggregations predicted by the model versus presence or absence observed from baited video drops. Includes all 211 drops at east Oahu.

	Predicted by model		
Observed	Aggregations absent (<5)	Aggregations present (≥5)	Percent correct
Aggregation absent	73	48	60
Aggregation present	19	71	79
			68 overall

Abundance of juveniles in the archipelago

Fishing surveys at insular slopes other than east Oahu (total 332 km) detected few juveniles (Table 5). Five of these sites (with snappers) were surveyed with video camera to compare with the east Oahu aggregations. Significant numbers of snappers were found only at a site off the southwest end of the island of Molokai (Sept 1993). A repeat video survey indicated that the significant between-station differences in snapper abundance initially reported at South Molokai, persisted 7 months later (K-W, χ^2=50.8, P<0.05) (Fig. 6).

The video index and CPUE of the conventional fishing gear were roughly consistent for all sites (Table 6). Snapper abundance was found unrelated to substrate type (r_s=0.59, P=0.40, n=7) or distance from the 15-m isobath (r_s=–0.84, P=0.15, n=7). However, distance/depth of discharge at the four sites with known sources of coastal drainage (Kaneohe, Kailua, S. Molokai, and Hanalei) were associated with snapper abundance (r_s=–1.0, P<0.001, n=4).

Video- and catch-based production estimates

Video abundance data from MHI sites at N. Molokai, Hanalei, and Kahului yielded a mean estimated den-

Table 5

Fishing effort, length of slope fished, and total snappers caught on surveys of Hawaiian insular slopes for juvenile snappers.

Island	Bottom trawls 1990 (no.)	Bottom longlines 1992 (no. hooks)	Fish traps 1989–94 (no.)	Handlining 1993–94 (line-hr)	Length of slope fished (km)	Total snapper caught (no.)
Oahu[1]	16 (5)[2]	— (150)	27 (53)	60 (50)	164 (14)	16 (828)
Molokai	26	—	101	87	60	256
Maui	6	150	—	—	16	4
Lanai	6	—	—	—	16	0
Kauai	—	150	—	—	18	3
Necker	—	—	25	—	16	0
FFS[3]	—	—	63	—	42	5
Total	54	300	216	147	332	284

[1] The east Oahu study site values are not included in any of the figured totals.
[2] Numbers in parentheses represent additional values from gear validation test done at the east Oahu site.
[3] FFS = French Frigate Shoals.

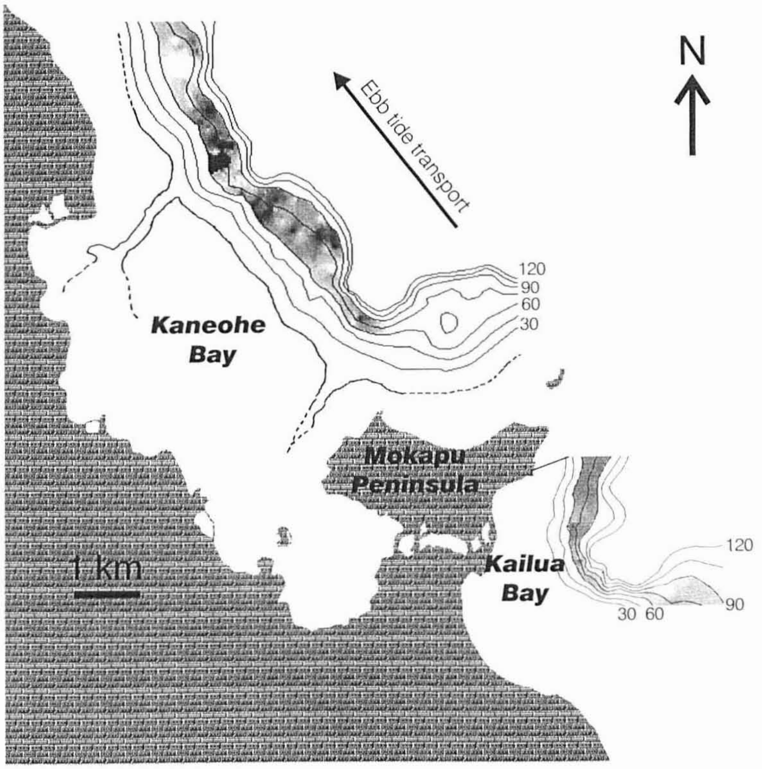

Figure 5

Interpolation of snapper abundance from all video deployments at the east Oahu study site (north Kaneohe, south Kaneohe, and Kailua). Increasing snapper abundance is signified with darker shading. Both north and south channels of Kaneohe Bay are contoured on the map, and a line is used to indicate the eastward extension of the Kailua outfall from the Mokapu pennisula. Isobaths are in 15-m intervals.

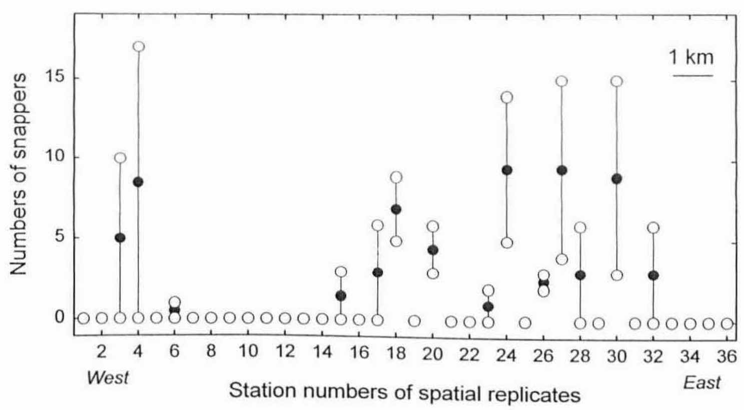

Figure 6

Mean (filled circle) and range (hollow circles) of number of snappers seen per video drop on south Molokai coastline survey. Each station received two video deployments. The drainage from the Kahanui swamp enters the ocean ~1 km to the east of extreme right of the graph.

sity of 6.6 snappers/km^2, which was taken as representative of routine "nonpremium" habitat. Assuming this density and a uniform distribution of snappers at a large scale, we estimated that the 2,600 km^2 of available habitat at 60–90 m depth in the MHI is equivalent to 17,200 juvenile snappers. This video-based estimate is no more than 15% of the 115,600–189,200 juvenile snappers (44–72 snappers/km^2) backcalculated from catch in the commercial fishery. A pilot study of recreational fishing[6] suggests that if recreational catch was included in the back calculation, the difference between video and catch estimates could be as high as one order of magnitude.

Discussion

Premium nursery habitat

Persistence of specific snapper aggregations on east Oahu was supported by both the multicanyon and multiyear analyses. However, because no multiyear surveys extended beyond the north Kaneohe site, we can only assume that year-to-year variability in the other east Oahu sites was similar. A strong year class of snappers might be expected to force some individuals to occupy marginal habitat, making the distinction between snapper aggregations less clear. Results of the multiyear survey indicated that 1993 and 1994 were relatively poor years for recruitment of young snappers, suggesting that the observed snappers in the multicanyon stations occupied favorable habitat.

Slope showed no significant effect on the distribution of snappers, but relief did. The deep sediment deposits on the terraces preclude any undetected small-scale relief features to which juveniles might orient. The few areas where escarpment features protruded from the sediment layer were associated with ab-

[6] Hamm, D. C., and H. K. Lum. 1992. Preliminary results of the Hawaii small-boat fisheries survey. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Sci. Cent. Admin. Rep. H-92-08, 35 p.

sence of snapper aggregations in the logistic model. This finding supports the hypothesis that structural relief or its associated community represents conditions less favorable or more hazardous to the snappers (greater interspecific competition, risk of predation, etc.) (Johannes, 1978; F. A. Parrish, 1989). Expanses of uniform sediment bottom are obviously an important substrate feature. The relative scarcity of this habitat observed at depths <60 m at least partly explains the absence of snappers on the shallower (30–60 m) grounds.

Proximity to point sources of drainage and its relationship with the presence of clay-silt sediment can explain much of the snappers' longshore distribution. Work with first-year juveniles of species of *Pagrus* has demonstrated that substrate and associated water flow are important to habitat selection (Francis, 1995). Improved availability of food has been proposed as a reason for fish demonstrating habitat preferences (Sudo et al., 1983). Distributions of sediment particle sizes such as clay-silt have been shown to enhance the localized distribution of certain benthic invertebrate infauna (Fegley, 1988). A favorable localized sediment composition might contribute to an enhanced forage base for juvenile fish (Tito de Morais and Bodiou, 1984). However, these longshore variations in clay-silt abundance are simply indicative of the longshore differences in coastal water flow that disperse the flocculent clay-silt. The highest fraction of clay-silt is found at the seaward end of the north Kaneohe channel, where snapper abundance is high and bay drainage is most concentrated. The density of fish in Kailua is greatest near the wastewater outfall, where the clay-silt fraction is lowest. The outfall introduces and increases the frequency of drifting materials to the area, similar to the flow of natural drainage sources, but without creating a clay-silt dispersion field. For this reason, the logistic model excluded the variable

Table 6

Characteristics and results of longshore coastal surveys for snappers at 7 sites.

Location (year) and "figure ID number"	Longshore distance surveyed (sampling interval) (km)	Index of abundance: Video sampling mean no./video drop	Index of abundance: Conventional research fishing (mean no.) Longline set	Index of abundance: Conventional research fishing (mean no.) Trap set	Uniform sediment seen in survey (%)	Mean distance of video drops from 15 m isobath and range (km)	Source of coastal drainage (max. depth of source in meters)
Kailua, Oahu (1994) "1"	4.6 (1)	24.8	—	—	88	1 (0.61–1.3)	Kailua wastewater outfall (30)
Kaneohe, Oahu (1992–94) "2"	13.8 (0.5)	4.5	3.8	5.78	95	1.24 (0.64–1.6)	Kaneohe Bay, north and south channels (15)
South Molokai (1993–94) "3"	16.6 (0.5)	1.97	—	2.0	81	1.6 (0.87–3.9)	Kahanui swamp and fringing reef drainage (15)
Hanalei, Kauai (1992) "4"	18.5 (1.5)	0.22	0.20	—	52	1.5 (0.77–4.2)	Hanalei estuary
Kahului, Maui (1992) "5"	15.7 (1.5)	0.03	0.01	—	92	4.3 (1.6–10.5)	None known
North Molokai (1994) "6"	5.5 (0.5)	0	—	0.007	92	0.87 (0.64–1.2)	None known
French Frigate Shoals (1993) "7"	42.6 (1.5)	0	—	0.037	40	1.3 (0.92–2.3)	None known

Figure ID numbers listed in first column correspond with survey sites shown in Figure 1, I.

clay-silt. This finding suggests that the distribution of juveniles within the preferred uniform sediment habitat is related more closely to water flow than to sediment particle size. Similar enhanced abundances of fish associated with anthropogenic sources have been proposed elsewhere (Mearns, 1974; Monaco et al., 1992) and in Hawaii (Henderson, 1992; Grigg, 1994).

In video deployments at many study sites, snappers were observed routinely picking at items in the lower water column and mouthing the substrate. DeMartini et al. (1996) determined that juvenile snappers at the north Kaneohe canyon eat a mixture of gelatinous drift, demersal crustaceans (amphipods, etc.), and benthos (micromollusks, annelids, etc.). The majority of prey were <1 cm, of low motility, and bottom associated.

Habitats receiving drainage from shallower environments might have their food supply enhanced in at least two ways. First, fish may encounter and feed more frequently on suspended organisms and other materials flushed from shallower reef and estuarine environments (Gerber and Marshall, 1974). Second, the flow from shallow sources may elevate the organics in sediments, thereby enhancing production of the benthos that snappers eat. Changes in benthic fauna at comparable depths (50–200 m) have been documented in relation to the flux of organics in the water column—both in natural (Buchanan and Moore, 1986) and anthropogenic situations (Nichols, 1985). Benthos may also become enriched during large episodic movements of nutrient-rich bay sediment to localized areas in the snapper grounds. The significant interaction, identified by the logistic model, of clay-silt with proximity to drainage sources supports the notion of enhanced organic input to the benthic community provided by such drainage.

Distribution of juveniles in the archipelago

Conventional fishing on the insular slopes of the archipelago (332 km) identified few sites with juvenile snappers; the mode and median of the catch of juveniles from all the gear was zero. Except for aggregation sites at Oahu and Molokai, catches of juveniles occurred only in token numbers. In a 1967–68 demersal trawl survey (n=62), Struhsaker sampled ~90 km of relevant depths in the main Hawaiian Islands and similarly found the occurrence of juveniles to be infrequent and patchy. His catches of juvenile snappers had a mode of zero and median of one (Struhsaker, 1973).

The 5 sites other than east Oahu that were surveyed by video (Table 6) each had substrate and depths consistent with those at east Oahu; 2 had sources of drainage; but only 1, south Molokai, supported a snapper aggregation. South Molokai's Kahanui swamp, located within the island's extensive fringing reef complex, has a drainage channel similar in width and depth (15 m) to north Kaneohe Bay (U.S. Army Corps of Engineers, 1984). Its associated snapper aggregation is well situated to exploit the tidal drainage of the reef platform and swamp dispersed by westbound currents of the area[7] (Fig. 6). The Hanalei estuary, on the island of Kauai, probably fails to influence snapper depths because it discharges at a zone of high-energy mixing (~1 m depth) too far inshore from juvenile snapper grounds.[8] The site at Kahului, Maui, would have to have a very large coastal drainage feature to aggregate snappers; the distance between the snapper grounds and such a source would be twice that of the other sites surveyed. Presumably, any source of increased suspended materials (embayments, reef platforms, or atoll lagoons) could enhance snapper aggregations if depth, distance, and circulation characteristics focused water and increased the frequency of suspended materials close to juvenile grounds (Cyrus and Blaber, 1983; Birkeland, 1984).

Struhsaker, during his 1967–68 trawl survey, identified one location (north coast of Oahu) with catches as high as 180 individuals in one haul. The substrate at the site was composed of uniform sediment and received discharge from two north Oahu rivers. However, according to the surveys from the present work, the snapper depths at this site seem almost too far offshore (mean=4.5 km) to support an aggregation. Numerous attempts in 1990 (Table 5) to relocate this north Oahu aggregation with the same gear that was used in 1967–68 did not yield any snappers. Many changes that could have modified the suitability of this habitat for juveniles (e.g. heavy exploitation of the snapper stock [WPRFMC[2]]; collapse of the coast's large-scale irrigation-based agriculture and its drainage; effects of increasing relief on juvenile grounds from the accumulation of incidental ocean dumping) have occurred in the 22 years between the surveys.

Implications for the fish stock

Regardless of what factors create premium habitat, the implications for the snapper stock of the archi-

[7] Wyrtki, K., V. Graefe, and W. M. Patzert. 1969. Current observations in the Hawaiian Archipelago. Hawaii Institute of Geophysics HIG-69-15, 27 p. Hawaii Inst. Geophysics, 2525 Correa Rd., Honolulu, HI 96822.

[8] U.S. Geological Survey. 1993. Water resources data Hawaii and other Pacific areas, water year 1993. Water-data Report HI-93-1:78-79. U.S. Geological Survey, 677 Ala Moana Suite, Honolulu, HI 96813.

pelago are intriguing and potentially important. It is not clear how widespread such habitat (and associated high densities of juvenile snappers) may be in Hawaii; present surveys and those of 1967–68 suggest that it represents a minor fraction of all habitat at appropriate depths. Use of the observed mean density of snappers on other habitats (6.6 snappers/ km^2) produced an estimate of juvenile standing stock much lower than that derived from catch records. A possible explanation for the discrepancy is that an abundance of snappers use unidentified habitats significantly shallower or deeper than 60–90 m. However, extensive diving in shallower waters, observations from submersibles (Moffitt et al., 1989; Haight et al., 1993), and systematic trawl surveys of deeper waters (Struhsaker, 1973) have not disclosed juveniles in other depth ranges. Conceivably, areas at depths with less than prime habitat for juvenile snappers may support loose, mobile aggregations with large home ranges that are difficult to relocate. As of yet, no such aggregations have been documented.

According to the Kaneohe GIS data (Fig. 5), juvenile snappers occurred within an area of 8 km^2 and showed a median video-based density index of 7; therefore, Kaneohe is likely to support 450 snappers/ km^2 (68-fold above mean estimated density) or a total of 3,600 snappers. This finding suggests that recruits from premium habitats like Kaneohe can produce a significant percentage of the MHI juveniles. If Kaneohe snapper abundance values are applied to reconcile the difference between the estimates generated by video densities in nonpremium habitats and those obtained by fishery catches, between 9% and 15% of the MHI habitat would have to be of the premium type to account for the current commercial snapper catch. If recreational catch is considered, a larger fraction of total habitat must be of a premium type. Exploring the actual extent of this habitat and the adult stock's dependence on it should be a management priority and a major focus for future work.

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