A Comparative Study of Habitat Use by Young-of-the-year, Subadult, and Adult Rockfishes on Four Habitat Types in Central Puget Sound*

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Abstract.– Seasonal habitat use of young-of-the-year, subadult, and adult rockfishes (*Sebastes caurinus*, *S. maliger*, and *S. auriculatus*) were compared for four habitat types: high-relief rocky reefs, low-relief rocky reefs, high-relief artificial reefs, and sand/eelgrass. Diving surveys conducted December 1986 through October 1988 on two representative sites of each habitat type revealed significant seasonal changes in rockfish densities and habitat use. Young-of-the-year (YOY) recruitment varied between the two survey years: YOY were observed on all habitat types in the summer and fall of 1987, whereas they were observed at only one site (artificial reef) in a similar time period of 1988. High-relief rocky reefs had the most consistent densities of the three rockfish species, mostly fish >200 mm TL. Adult and YOY copper, quillback, and brown rockfishes were observed on the low-relief rocky reefs primarily in the summer months coincident with summer algal growth; when the kelp died back in the fall, most rockfishes left these reefs. The highest densities of rockfishes, primarily 80–200 mm quillback rockfish (up to 420/90-m^3 transect) and large copper rockfish (up to 56.3/transect), were observed on the artificial reefs. Here, also, density fluctuations were dramatic; copper rockfish densities peaked in fall and winter and declined (to 0/transect) during the summer, and quillback rockfish densities also seasonally fluctuated. Sand/eelgrass areas were the least-utilized habitat type; only during July and August were young-of-the-year and low densities of adult copper and brown rockfishes observed on one sand/eelgrass site. Although all four habitats were used, natural reefs may represent source habitats that are used by and maintain rockfishes on less productive sink (artificial reef) habitats. Thus, the recent use of artificial reefs as mitigation for the loss of natural reefs could have negative impacts on rockfish populations.

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Rockfishes are a successful group of marine fishes represented by about 100 species (Barsukov 1981), which occupy a variety of habitats ranging from the intertidal to the edge of the continental shelf (Lea 1983). This speciose and interesting group displays extremes in habitat use and movement patterns: Some species live deep (500 m) over sandy bottoms, some make long-distance movements (to 550 km), whereas others are perennially sedentary on shallow (<10 m) rocky reefs (Larson 1980, Love 1980, Culver 1987). One group of rockfishes is solitary and demersal and inhabits shallow reefs (Ebeling et al. 1980a); in Puget Sound this group of rockfishes is represented by copper *Sebastes caurinus*, quillback *S. maliger*, and brown *S. auriculatus*.

Copper, quillback, and brown rockfishes are common shallow-water benthic species found along the Pacific coast of North America (Hart 1973). They are morphologically similar to one another but differ in coloration. The three species have overlapping geographic ranges; copper and brown rockfishes are found from Baja California to Alaska, whereas quillback are found from central California to Alaska (Hart 1973). All three species occur in Puget Sound, Washington, and comprise approximately 25% of the recreational bottomfish catch in central Puget Sound (Palsson 1988). These species inhabit a variety of habitat types although highest densities are reported on artificial reefs, natural rocky reefs, and rock piles in water less than 30 m (Moulton 1977, Buckley and Hueckel 1985). Usually these species are found directly on the bottom closely associated with rock, artificial substrate, or vegetation (Patten 1973, Moulton 1977). Although copper and quillback rockfishes are common throughout Puget Sound, the San Juan Islands, and Strait of Juan de Fuca, brown rockfish are more limited in distribution and are found only within central and south Puget Sound (Moulton 1977).

Rockfishes are viviparous (Boehlert and Yoklavich 1984), undergoing internal fertilization and subsequently releasing pelagic larvae. Little is known regarding the length of time that young rockfishes are pelagic before they recruit to adult or transitional habitat. Parturition reportedly occurs April through June for the three species in Puget Sound (DeLacy et al. 1964, Washington et al. 1979, Dygert 1986). An influx of postlarval or young-of-the-year (YOY) rockfishes into isolated areas in Puget Sound has been observed (Patten 1973, Gowan 1983); assessment of habitat

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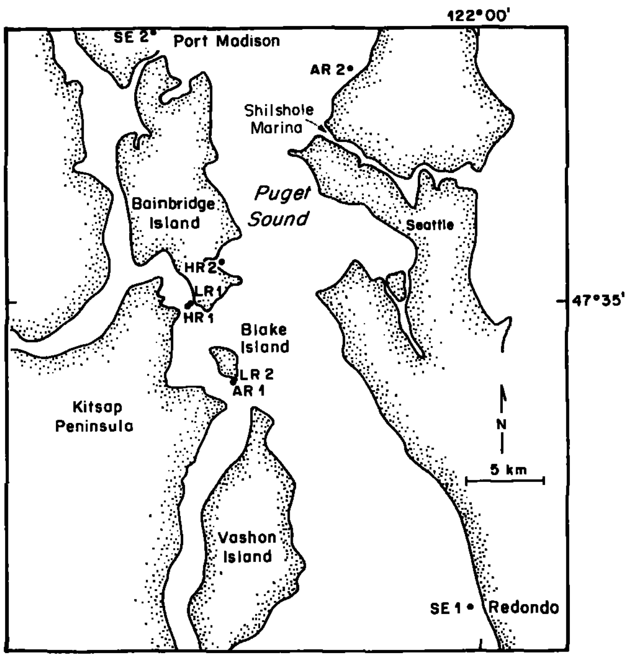

Figure 1
Map of study sites within central Puget Sound. HR1 Orchard Rocks, HR2 Blakely Point, LR1 Bainbridge Island, LR2 Blake Island, AR1 Blake Island, AR2 Boeing Creek, SE1 Redondo, SE2 Port Madison.

features required by recruits and different habitats utilized has been only qualitatively described. It is likely that habitat requirements of juveniles and adults differ, as juveniles may require shelter from predation and associate more closely with structural algal cover (Hobson 1972, Carr 1989). Ebeling and Laur (1985) experimentally demonstrated that young surfperches sought and were restricted to microhabitats that offered protection from predation. Carr (1983) suggested that kelp may provide a refuge from predation for YOY rockfishes including three species found offshore as adults (*Sebastes paucispinus*, *S. pinniger*, and *S. miniatus*), that recruit to kelp beds in central California. Because rockfish produce pelagically dispersed larvae and juveniles, local adult density is probably a poor predictor of local recruitment and future adult density. Rather, the limited availability of habitat with which young-of-the-year and juvenile associate may be the critical determinant of local recruitment. Determining the habitat requirements of young rockfishes can be crucial to our understanding of local rockfish dynamics. If algae, seagrasses, or other habitats provide YOY rockfishes essential shelter from predation and increased access to food, then recruitment could be suppressed by eliminating such shelter or enhanced by adding more shelter. Habitat affinities and requirements are an unknown for YOY and juvenile rockfishes in Puget Sound.

Copper, quillback, and brown rockfishes inhabit a variety of habitats, yet the relative importance of each habitat and seasonal uses are unknown. Additionally, differences in habitat use by different life-history stages are poorly understood. For example, do young rockfishes settle on reefs and remain there for life, or do the different age groups (young-of-the-year, subadult, and adult) later move to separate or different habitats? Understanding how and when the different habitats are exploited provides needed information on ecological requirements for habitat management; recognition and protection of important habitats are necessary for effective fisheries management. Similarly, further descriptions of the different habitats are required to adequately assess the relative importance of habitat features to the different life-history stages of rockfishes. This study was designed to provide a quantitative comparison of habitat use for copper, quillback, and brown rockfishes on four habitat types common in Puget Sound.

Materials and methods

Study sites

For each of four habitat types—high-relief rocky reef, low-relief rocky reef, high-relief artificial reef, and sand/eelgrass—two representative replicate study sites were selected. The two high-relief natural rocky reefs were characterized by steep vertical relief to 5 m off the bottom, surface canopies of the annual bull kelp *Nereocystis leutkeana* May through November, and understories of the perennial kelps *Agarum fimbriatum* and *Pterygophora californica*. The high-relief rocky reefs range in depth from 12–20 m (gauged from mean lower low water). The Orchard Rocks high-relief rocky reef (HR1) is located on the southeastern side of Bainbridge Island (Fig. 1) approximately 600 m offshore in the middle of Rich Passage, which is swept by high currents up to 8.1 km/hour (4.5 knots) (U.S. Dep. Commer. 1987, current tables). The entire Orchard Rocks reef covers approximately 5 ha. The portion of reef used as the study site was about 12–18 m in depth and consisted of large boulders and rocky ledges that rise up to 5 m off the bottom. The second high-relief reef (HR2), Blakely Point, is a series of rock outcroppings separated by sand and shell gravel. The outcroppings are oriented perpendicularly offshore from the north entrance of Port Blakely Harbor on the eastern side of Bainbridge Island. Transects extended across the reef from 12–18 m in depth; each transect covered a similar depth range. Similar to HR1, the HR2 reef consists of steep walls and crevices with vertical relief of 5 m, but has minimal current.

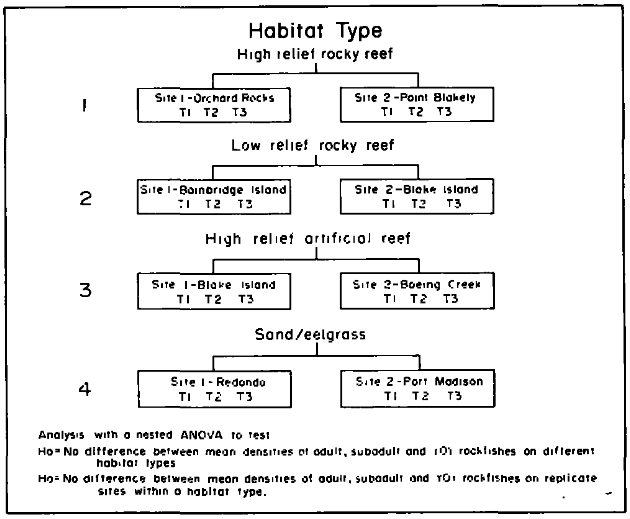

Figure 2
Nested experimental design showing habitat types in central Puget Sound, sites within habitat types, and the three transects per site.

The two low-relief rocky reefs were characterized by flat, featureless cobble and rock bottom with a few isolated areas of vertical relief (1–2 m). Transects extended from 8–10 m in depth, but not deeper than 10 m where the reef drops off into sand/cobble substrate. The low-relief reefs were more uniform in depth when compared with the high-relief reefs. Both low-relief reefs have dense canopies of *Nereocystis leutkeana* May through November and understories of perennial kelps *Agarum fimbriatum* and *Pterygophora californica*. Low-relief habitats underwent dramatic changes in the fall and winter when they were virtually devoid of all fish and algal structure. Bainbridge Island low-relief rocky reef (LR1) is 500 m inshore from HR1, and the two reefs are separated by cobble and sand. Blake Island low-relief reef (LR2) is located 5 km south of Bainbridge Island. Both low-relief reefs are swept by high currents up to 8.1 km/hour (4.5 knots).

The two high-relief artificial reefs were characterized by vertical relief of up to 5 m and no surface canopies of bull kelp, but with isolated patches of understory kelps. Transects extended from 15–20 m in depth. The Blake Island artificial reef (AR1) was constructed in 1980 (Laufle 1982) and is located 5 km south of Bainbridge Island on the southwestern side of Blake Island approximately 500 m offshore of LR1. The reef consists of concrete rubble, slabs, rectangular boxes, and tires forming vertical relief up to 4 m. The Boeing Creek artificial reef (AR2) was constructed in late 1982 and is located 8 km north of Shilshole marina approximately 600 m offshore. The reef consists of concrete rubble with vertical relief of up to 6 m. The two reefs differ, as Blake Island is swept by strong currents up to 8.1 km/hour (4.5 knots) while Boeing Creek experiences little current.

The sand/eelgrass areas were characterized by flat, shallow, unconsolidated substrate with dense growth of eelgrass *Zostera marina* May through November. Eelgrass typically grows in low-current, sheltered water and is restricted to depths less than 6 m (Phillips 1984), so the transects were placed at 5 m. The Redondo (SE1) sand/eelgrass area is located approximately 500 m north of Saltwater State Park, 24 km south of Seattle. The Port Madison eelgrass area (SE2) is located 500 m north of the Suquamish boat ramp, off the northern side of Bainbridge Island.

Survey methods

From December 1986 through February 1988, I conducted monthly SCUBA surveys and estimated rockfish densities along three (30-m long, 3 m wide, and 1 m high) permanent transect lines at each of the eight reefs (Fig. 2). After the February 1988 survey, surveys were conducted in April, June, July, and August of 1988. In October 1988, surveys quantifying only YOY rockfishes were conducted on four reefs where YOY had been observed in the summer and fall of 1987: HR2, LR1, AR2, and SE2. All eight sites were sampled each month, and all three transects were sampled on the same day. I swam along the transect line and recorded individuals of each species as YOY (<80 mm TL), subadult (80–200 mm TL), and adult (>200 mm TL). During the summer and early fall when kelp cover was the highest, I also swam through the canopy to search for YOY rockfish. The ability to designate these size categories was verified by periodically capturing and measuring fish. Because YOY copper, quillback, and brown rockfishes could not be identified to species underwater, they were combined into one group. A total of 456 transects was completed on all reefs: 24 transects conducted monthly for 15 consecutive months December 1986–February 1988, and 24 transects conducted monthly during April, June, July, and August 1988. Fifteen additional YOY surveys were completed in October 1988.

Other information collected along the transect lines included estimates of vegetative cover and water temperature. Kelp and eelgrass cover was qualitatively assessed by estimating, at the end of each transect, the percent cover of bullkelp, understory kelps, and the height of eelgrass present. The percent cover ranged from 0 (no vegetation present) to 100% (transect line completely covered by vegetation). Temperatures were recorded along the transect lines on each survey with a submersible thermometer.

Survey analyses

From the three transects at each site, a mean number (±95% CI) of fish per transect was computed for each species and size category. To determine whether densities of rockfishes differed among the four habitat types and within the two replicate sites within each habitat type, I used a nested analysis of variance (ANOVA) (Zar 1984) (Fig. 2) that tested two null hypotheses: (1) There is no difference in rockfish densities between habitats ($F_{0.05(1)3\,(\text{habitat types}),\,4\,(\text{sites})}$), and (2) there is no difference in rockfish densities between the two replicate sites within each habitat type ($F_{0.05(1)4\,(\text{sites}),\,16\,(\text{error})}$). The degrees of freedom for error was calculated as (4(types) · 2(sites) · 3(transects) − 4 · 2) = 16 (Zar 1984, p. 147). To reduce the number of analyses, data were analyzed as a separate ANOVA for each of six seasonal periods using the middle month: Winter 1 = December 1986–February 1987; spring = March 1987–May 1987; summer 1 = June 1987–August 1987; fall = September 1987–November 1987; winter 2 = December 1987–February 1988; and summer 2 = June 1988–August 1988. Although density estimates were similar within quarters (Figs. 3–6), the sedentary behavior of rockfish could mean that the same individuals were counted in February that had previously been counted in January, which would constitute a repeated sample. Thus to eliminate the possibility of non-independence of data, as I have no evidence that rockfish redistribute themselves randomly from month to month, I used only the middle month of each quarter. Because many months and sites contained zero densities and, in some cases, the variances were proportional to the means, the data were transformed using a square root transformation (X' = square root (X + 0.5)). If a significant difference in densities was detected among the four habitat types, the types were then compared using Tukey's multiple range test (Zar 1984) to determine which types were different.

To determine whether densities were different between years at each site, quarterly estimates were compared using a Student's t-test (Zar 1984). For these tests, densities from the summer of 1987 were compared with the summer of 1988 for each site testing the null hypothesis: There is no difference between densities of each site between summer 1987 and summer 1988. Similarly, densities from the winter of 1987 were compared with the winter of 1988. I conducted individual tests for copper, quillback, brown, and YOY rockfishes for summer and winter comparisons.

Results

Habitat type and site comparisons

All size categories of copper, quillback, and brown rockfishes and YOY rockfish were seen at the high-relief natural habitat type (Fig. 3). Consistent monthly densities of large (>200 mm) copper (mean 3.7–13.0 fish/90-m^3 transect) and quillback (mean 3.0–7.0 fish/transect) rockfishes were observed throughout the year on the high-relief rocky reefs. Brown rockfish (>200 mm) (mean 1.3–4.0 fish/transect) were seen at HR1 (Orchard Rocks) but infrequently at HR2 (Blakely Point). Low densities (mean<1.3 fish/transect) of subadult (80–200 mm) copper, quillback, and brown rockfishes were observed on both reefs until the late summer and fall 1987. YOY (<80 mm) rockfishes were observed (mean 8.0–57.0 fish/transect) from August–November 1987 but only on HR2. YOY were not observed in the summer or fall of 1988. After the influx of YOY during summer and fall 1987 on HR2, an increase in 80–200 mm rockfishes was subsequently observed (mean 6.0–15.0 fish/transect).

Rockfishes primarily utilized low-relief rocky reefs during the summer, coincident with peak *Nereocystis leutkeana* and understory cover, and were infrequently observed during other seasons (Fig. 4). Large copper (up to a mean 6.0 fish/transect) and brown rockfishes (up to a mean 7.7 fish/transect) were observed mainly during the summer, whereas large quillback rockfish were not seen at LR1 and only infrequently at LR2. Low densities (mean 0–3.3 fish/transect) of small copper and quillback rockfishes were seen on LR2, while small brown rockfish were never seen on either reef. YOY rockfishes were observed (mean 16.7 fish/transect) during August 1987 on LR1 and (mean 1.3 fish/transect) on LR2 during October 1987, but not during the summer or October of 1988.

On the artificial reefs, densities of large copper rockfish fluctuated throughout the year. During both 1987 and 1988, high densities (mean 12.0–56.3 fish/transect) were seen September through May; however, low densities (mean 0.3–2.3 fish/transect) of copper rockfish were observed June through August (Fig. 5). Variable densities (mean 0–12.3 fish/transect) of large quillback rockfish were observed on AR1 while they were lower in number (mean 0–2.3 fish/transect) on AR2 (Fig. 5). Large brown rockfish were infrequently (mean 0–0.3 fish/transect) seen on either artificial reef. Low densities (mean 0–5.0 fish/transect) of subadult (80–200 mm) copper rockfishes were observed on both artificial reefs throughout the year. Extremely high densities (mean 8.0–420.0 fish/transect) of subadult quillback rockfish were observed on both AR1 and AR2, although densities were much higher on AR2 (up to 420

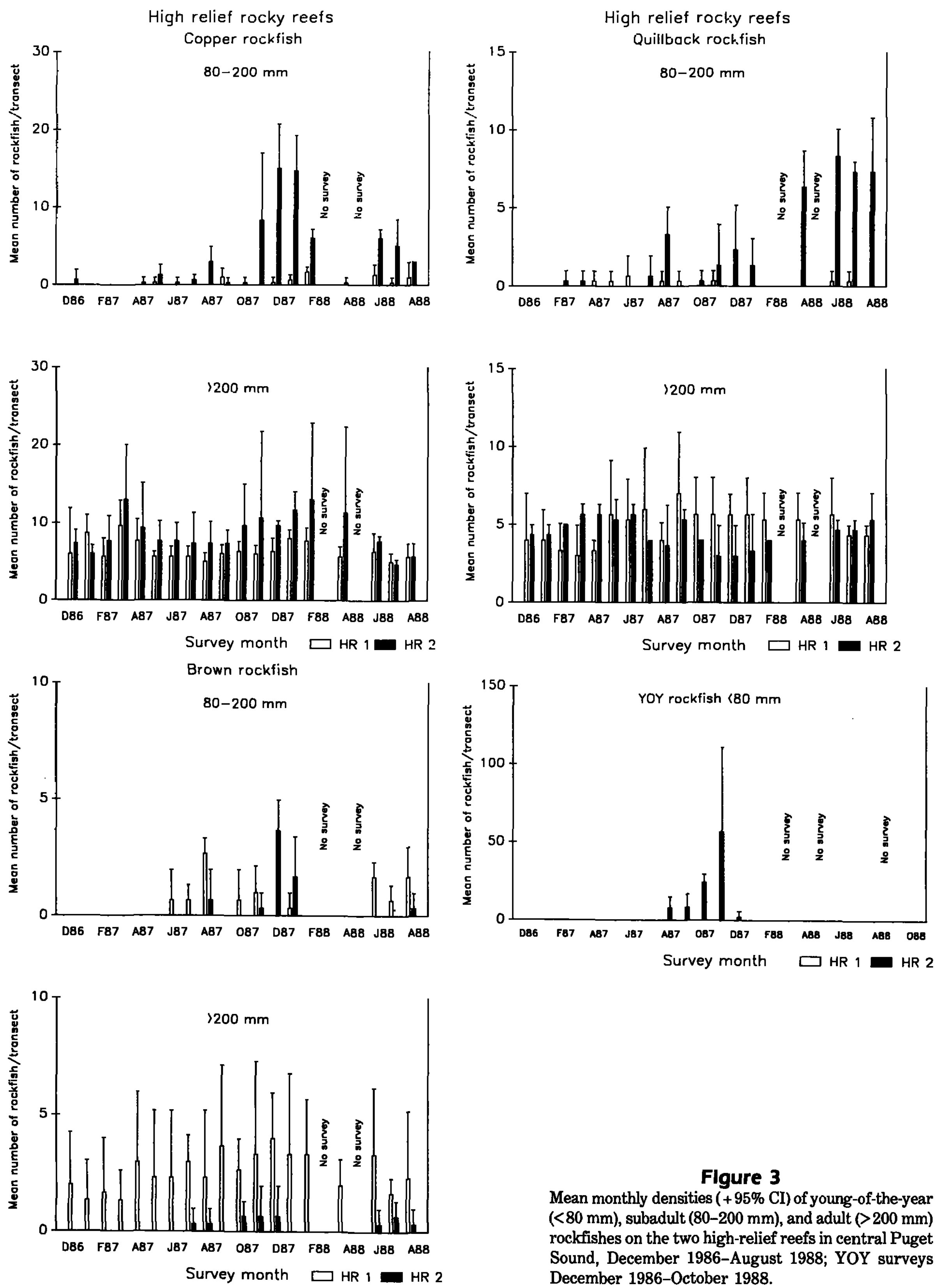

Figure 3

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two high-relief reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988.

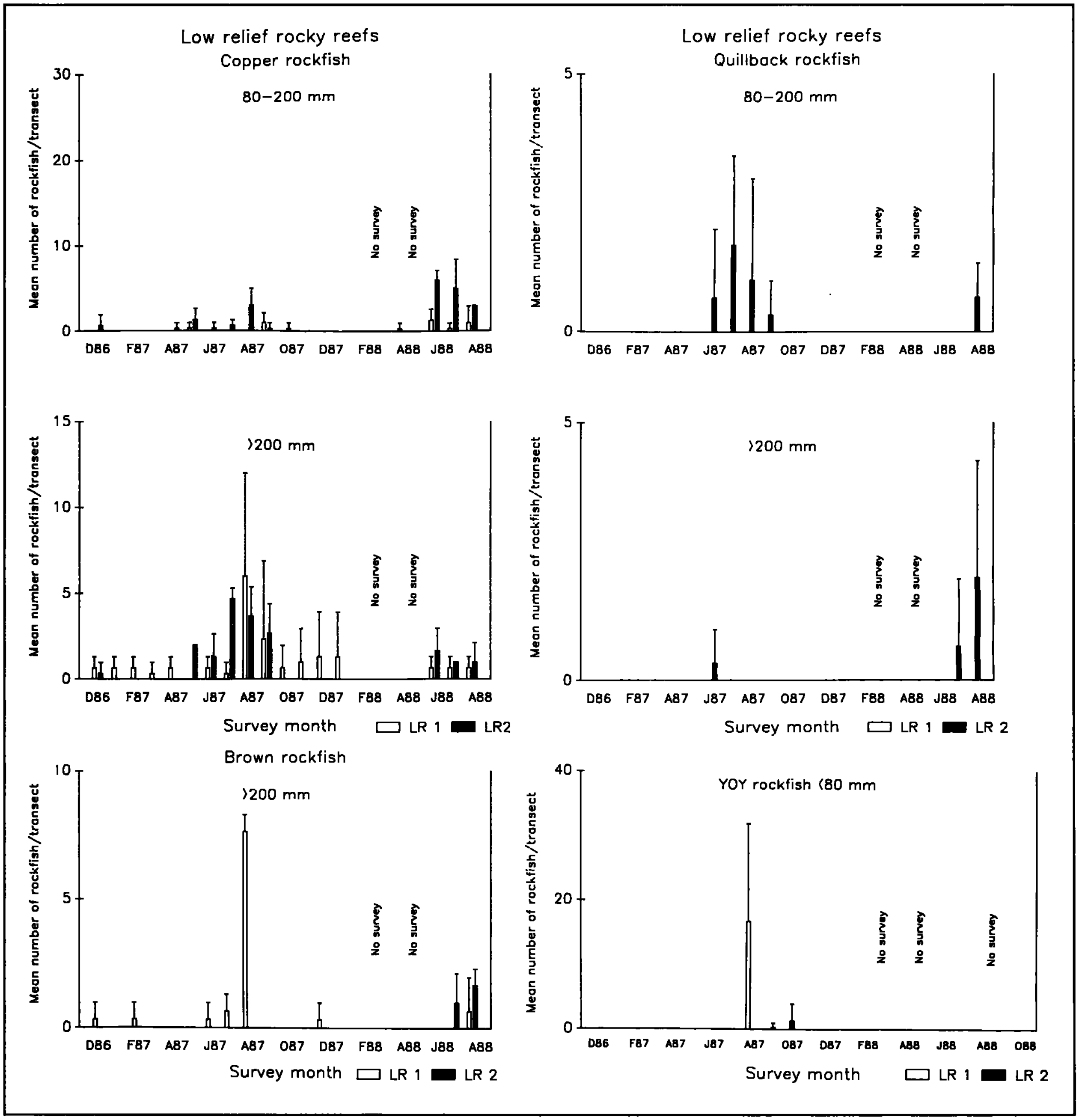

Figure 4
Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two low-relief reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988. No subadult brown rockfish were observed.

fish/transect). Small brown rockfish were infrequently (mean 0–0.3 fish/transect) seen on either artificial reef. YOY rockfishes were observed (mean 1.7–63.0 fish/transect) only on AR2 during the spring of 1987, and during the following fall, winter, spring, and summer (mean 4.3–80.0 fish/transect). Low densities (mean 2.0 fish/transect) were observed in the October 1988 survey. YOY were never observed on AR1.

Sand/eelgrass areas had the lowest densities of all habitats sampled; large copper rockfish (mean 5.0 in July 1987, mean 0.7 in August 1988), brown rockfish (mean 1.0, August 1987) and YOY (mean 111.0, July

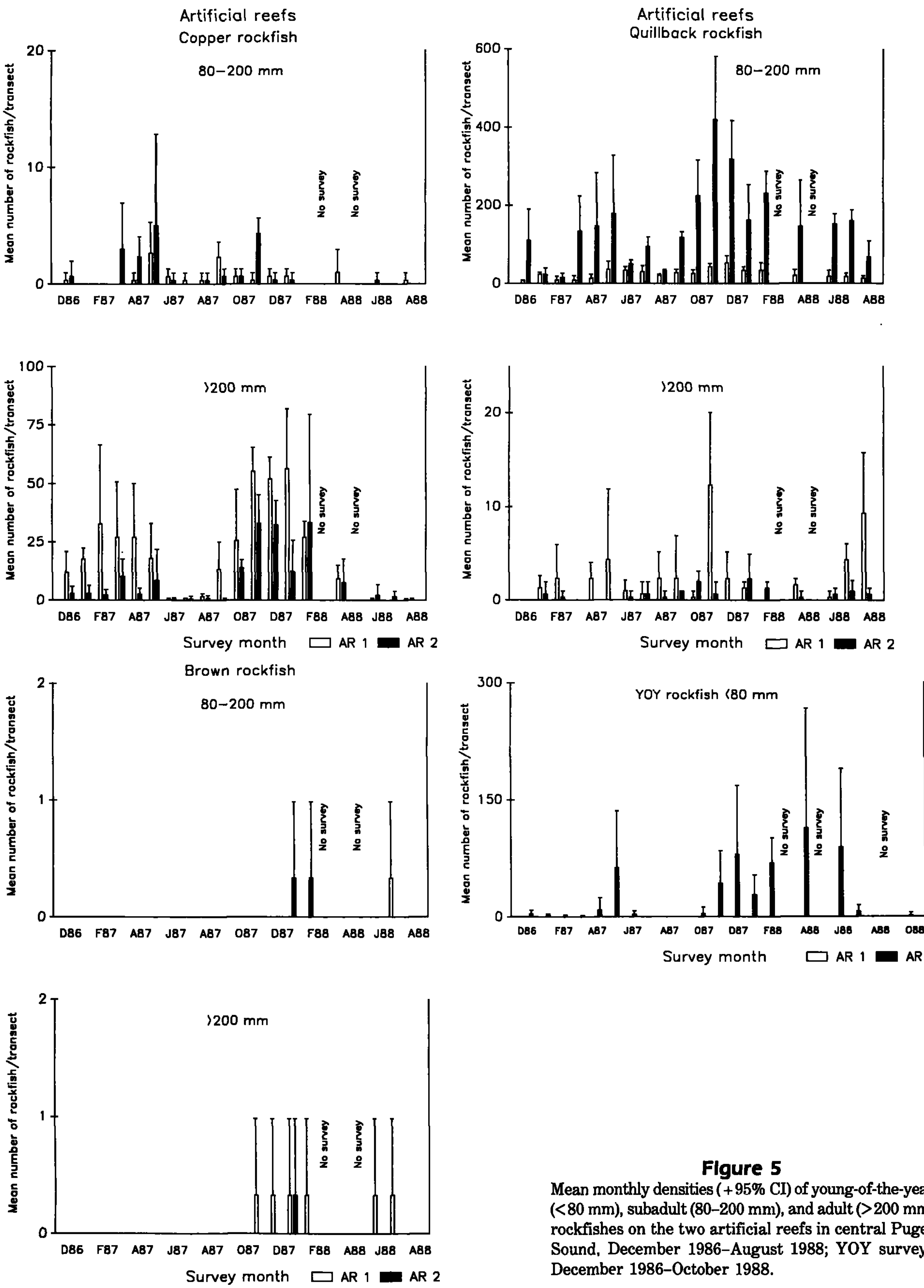

Figure 5

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two artificial reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988.

1987) were the only rockfishes seen and only during surveys conducted in late July and August (Fig. 6). These observations of rockfishes coincided with the peak growth of eelgrass up to 1.5 m high; in the fall and winter the height of eelgrass beds was reduced to <0.5 m. No quillback rockfish were ever observed on sand/eelgrass.

Nested analysis of variance

Habitat type comparison When density differences were detected, the highest densities were observed on the high-relief rocky and artificial reefs ($P<0.05$ nested ANOVA, Table 1). Highest densities of large copper rockfish were observed on high-relief rocky reefs during both the summer of 1987 and 1988, whereas artificial reefs had the highest densities in the fall and winter. Similar low densities of 80–200 mm copper rockfish were observed on all four habitat types all seasons except fall 1987. High-relief rocky reefs had the highest densities of large quillback rockfish all seasons; sand/eelgrass and low-relief rocky reefs were similar as large quillback rockfish were rarely observed. Artificial reefs had the highest densities of 80–200 mm quillback rockfish all seasons except winter and summer 1988. No density differences were observed for both size groups of brown rockfish on any of the habitat types. Similarly, YOY rockfishes were observed on all four habitat types, and no differences were detected in densities of YOY rockfish among the four habitats.

Replicate site comparison For many (23/42 groups) size groups of copper, quillback, brown, and YOY rockfishes, there were significant differences in densities between the two replicate sites for most seasons ($P<0.05$ nested ANOVA, Table 1). The major exception was that similar densities of large copper rockfish were observed on replicate sites all seasons except spring 1987.

Year-to-year comparison

For most size categories of copper, quillback, and brown rockfishes, there were no significant difference between their densities for the two periods tested: Summer 1987–summer 1988, and winter 1987–winter 1988 (Table 2). For the summer comparisons, the principal differences in densities were for YOY rockfish on all sites where they were observed: HR2, LR1, LR2, AR2, and SE2. YOY were observed at all five reefs in the summer of 1987; however, no YOY were observed in the summer of 1988, except at AR2. Other differences between summer 1987–1988 densities were 80–200 mm quillback rockfish on HR2; densities of small quillback rockfish were higher in the summer of 1988 after the YOY recruitment of 1987.

Similar to the summer 1987–summer 1988 comparisons, there were few significant density differences for winter 1987–winter 1988 (Table 2). The principal differences were that large copper rockfish and small

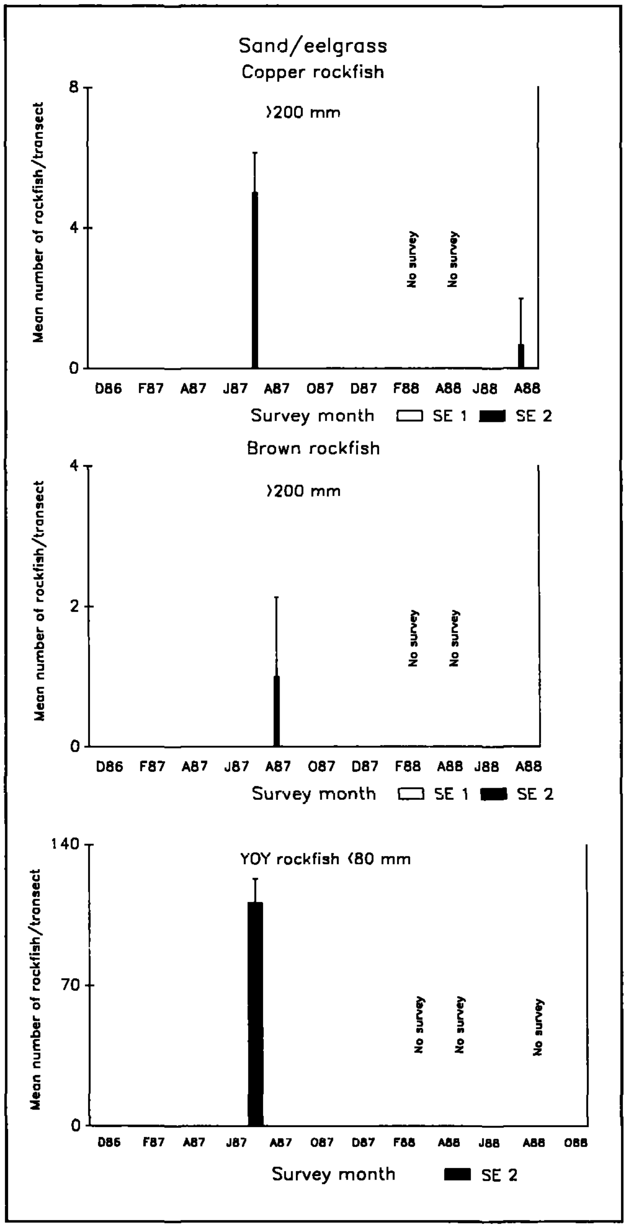

Figure 6
Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two sand/eelgrass areas in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988. No quillback rockfish (80–200 mm or >200 mm), subadult copper rockfish, or subadult brown rockfish were observed.

Table 1

Results of the nested ANOVAs ($P<0.05$) testing for differences between rockfish densities among the four habitat types: High-relief rocky reef (HR), low-relief rocky reef (LR), high-relief artificial reef (AR), and sand/eelgrass (SE). If there was a significant difference between type densities (Test 1), the results of Tukey's multiple range test are listed from highest to lowest densities. Test 2 lists the significant differences (*) in densities between sites.

	Copper		Quillback		Brown		Young-of-the-year
	80–200	>200 mm	80–200 mm	>200 mm	80–200 mm	>200 mm	<80 mm
Test 1							
1987							
Winter			AR>HR>SE=LR	HR>AR>LR=SE			
Spring			AR>HR>SE=LR	HR>AR>LR=SE			
Summer		HR>LR>AR=SE	AR>HR>SE=LR	HR>AR>LR=SE			
Fall	AR>HR>LR=SE	AR>HR>LR=SE	AR>HR>SE=LR	HR>AR>LR=SE			
1988							
Winter		AR>HR>LR=SE		HR>AR>LR=SE			
Summer		HR>LR>AR=SE		HR>AR>LR=SE			
Test 2							
1987							
Winter							*
Spring	*	*	*	*		*	
Summer			*		*	*	*
Fall			*	*		*	*
1988							
Winter	*		*			*	*
Summer	*		*	*		*	*

Table 2

Summary of year-to-year comparisons testing (Student's t-test) for differences in rockfish densities between summer (June, July, Aug.) 1987–summer 1988 and winter (Dec., Jan., Feb.) 1987–winter 1988. Listed are habitat types where a significant difference was detected. HR = high-relief rocky reef, AR = high-relief artificial reef, LR = low-relief rocky reef, SE = sand/eelgrass.

	Summer 1987–Summer 1988	Winter 1987–Winter 1988
Copper		
80–200 mm	HR2	HR2
>200 mm	AR1	HR2, AR1, AR2
Quillback		
80–200 mm	HR2, AR1, AR2	AR1, AR2
>200 mm	No differences	HR1
Brown		
80-200 mm	No differences	HR2
>200 mm	LR1	No differences
Young-of-the-year		
<80 mm	HR2, LR1, LR2, AR2, SE2	AR2

quillback rockfish densities were higher in the winter of 1988 on both artificial reefs. In addition, both small and large copper rockfish increased on HR2.

Species comparison

Small copper rockfish were infrequently seen on any habitat (Figs. 3–6). Small copper rockfish were first observed on the high-relief rocky reefs after the influx of YOY in the fall and winter. They were also sporadically observed on the artificial reefs and Blake Island low-relief reef. Large copper rockfish were seen on all habitat types and were observed all seasons. Consistent densities of large copper rockfish were observed

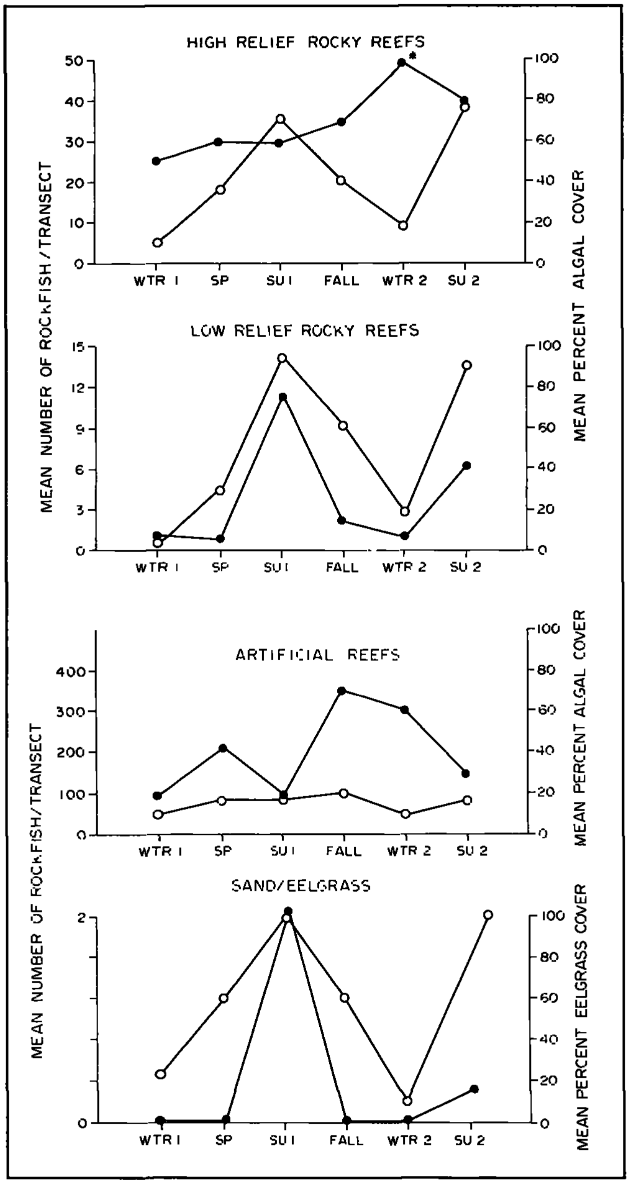

Figure 7
Mean percent of algal or eelgrass cover (O) compared with mean number (●, combination of 80–200 mm and >200 mm) of copper, quillback, and brown rockfishes on the four habitat types in central Puget Sound for winter 1 (wtr1), spring (sp), summer 1 (su1), fall (fall), winter 2 (wtr2), and summer 2 (su2). Seasons are described in Methods section. Density increase in high-relief rockfish (*) followed the influx of young-of-the-year rockfish. Percent eelgrass cover was relative to maximum height (1.5 m) of eelgrass which occurred during the summer.

on the high-relief reefs all seasons. In contrast, their densities fluctuated seasonally on other habitats; they were only observed during the summer and fall on the low-relief reefs during all seasons, although in lower densities during the summer on the artificial reefs, and only during the summer on the sand/eelgrass.

Small quillback rockfish were primarily observed on the artificial reefs all seasons and were infrequently observed on all other habitats (Figs. 3–5). Large quillback rockfish were most common on the high-relief rocky reefs and artificial reefs. Large quillback rockfish were rarely observed on the low-relief reefs. Neither small nor large quillback rockfish were observed on the sand/eelgrass.

Small brown rockfish were observed only on the high-relief reefs and on one artificial reef (Figs. 3, 5). Large brown rockfish were seen all seasons on the high-relief reefs although highest numbers were observed at HR1 (Orchard Rocks) (Fig. 3). They were also seen during the summer on low-relief reefs and sand/eelgrass (Figs. 4, 6).

YOY rockfish were observed on all four habitat types (Figs. 3–6). On the high-relief, low-relief reefs, and the sand/eelgrass, they were first seen in the summer and fall of 1987. YOY were observed year-round on Boeing Creek artificial reef. YOY were not observed in the summer or October of 1988 except at AR2.

Macrophyte cover varied seasonally; the densest cover was observed June through October on all reefs (Fig. 7). The high-relief reefs had dense canopies of *Nereocystis leutkeana* and subcanopies of *Pterygophora californica*, and *Agarum* that during the summer covered 50–100% of the bottom along the transect lines. The two low-relief reefs had 100% bullkelp and understory coverage June through October. The annual bullkelp was gone November through May and only the stipes of the understory perennial kelps remained; the blades of the understory kelps had eroded or were otherwise lost. There was no *Nereocystis* on the two artificial reefs; however, understory kelps covered approximately 0–20% of the transects, with peak growth in the summer. Sand/eelgrass transects were always covered with the perennial eelgrass throughout the year, although the height varied seasonally. The height peaked during the summer at approximately 1.5 m, and during the winter many of the blades were gone and the eelgrass was prostrate with little (0–0.5 m) vertical structure.

Monthly mean temperatures were highest August through October (up to 13°C) and lowest (down to 7.1°C) in January and February (Fig. 8). There was little qualitative difference in temperatures between the different reefs, although depth ranges were 5–20 m along transect lines.

Discussion

Seasonal habitat use

Habitats that underwent seasonal vegetation and subsequent structural changes had the most dramatic

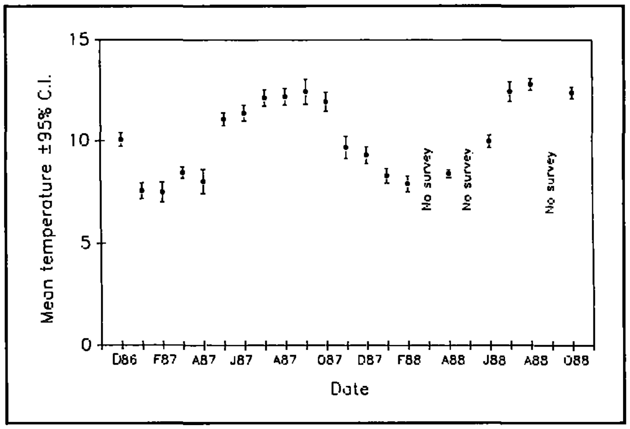

Figure 8
Mean monthly bottom temperatures (°C) ±95% CI measured along transect lines on the eight reefs in central Puget Sound, December 1986–October 1988.

density differences (Fig. 7). On the low-relief rocky reefs and sand/eelgrass, the highest densities, mainly >200 mm copper, brown, and YOY rockfishes, were observed during the summer coincident with the densest growth of bull kelp, understory kelps, and eelgrass. When the vegetation died back, lowest densities of rockfishes were observed, presumably due to movement away from the reefs. Movement away from the Blake Island low-relief reef in the fall onto the Blake Island artificial reef was confirmed in a tag-recapture study (Matthews In press). Richards (1987) also noted a decrease in copper rockfish densities off Vancouver Island during the winter, but argued that it was not fish movement that caused the decrease in densities but rather that during the winter fish were simply more difficult to see as they presumably hid in crevices. On the low-relief reefs and sand/eelgrass areas I surveyed, this explanation was not the case. Once the vegetation died back there were few places for fish to hide undetected by divers; there are no crevices or holes in the flat-bottom rock reef and sand. Fishing pressure was not responsible for the seasonal density fluctuations. Although I never directly measured the amount of fishing activity, I observed the highest number of sportfishing boats (both divers and anglers) at the high-relief reefs, whereas the lowest fishing effort occurred at the low-relief and artificial reefs. Larson and DeMartini (1984) compared two low-relief areas in southern California with and without giant kelp *Macrocystis pyrifera*. They found a higher biomass of fishes on the reef with kelp and concluded that the presence of kelp on low-relief reefs enhances fish biomass by providing prey and structure. The seasonal change in kelp on high-relief reefs had no effect on fish densities; presumably there is adequate structure (rocks and crevices) and prey on these reefs regardless of kelp cover. Other research in California has demonstrated that kelp on high-relief reefs had less effect on fish abundance when compared with their dramatic effect on low-relief reefs; when kelp cover declines on low-relief reefs, the shelter is lost but refuge in high-relief rock is permanent regardless of kelp cover (Quast 1968, Stephens et al. 1984, Ebeling and Laur 1988). Large (>200 mm) copper rockfish densities on the artificial reefs declined dramatically during the summer coincident with higher densities of large copper rockfish on the low-relief rocky reefs. Copper rockfish may leave the artificial reefs in the summer because of the lack of vegetation (bullkelp and understory kelps) and its associated prey. The summer is an important feeding time for rockfishes when fat reserves are stored to be used as energy sources during the winter (Guillemot et al. 1985). Although the artificial reefs had isolated patches of perennial kelps (*Agarum* and *Pterygophora*) during the summer, this habitat type had the sparsest vegetation growth of all the habitats surveyed. Because low-relief rocky reefs, artificial reefs, and sand/eelgrass were not suitable year-round habitats, rockfish move to utilize alternate habitats during the winter (Matthews In press).

Habitat comparison

Apparently, high-relief rocky reefs were suitable habitat for copper, quillback, brown, and YOY rockfishes: This was the only habitat type where all size categories of the three species as well as YOY were observed, although few were observed in the 80–200 mm range. Actually, one should not expect to see high numbers of 80–200 mm rockfish. Copper and quillback rockfishes are relatively slow-growing and may live up to 55 years (Richards and Cass 1987). Rockfishes release thousands of larvae, and the highest predation and mortality is on the youngest fish; presumably only a few survive to adults. Rockfish >200 mm represent several age groups—those rockfish about 5 years and older—whereas the 80–200 mm group represents only a few age classes of 1–5 years (Sandra Oxford, Wash. Dep. Fish., Seattle, WA 98115, pers. commun., summer 1988). Thus, one would expect to see more fish >200 mm than 80–200 mm on the high-relief natural reefs where the size groups co-occur. High-relief rocky reefs also had the most consistent densities of large rockfish and were the most structurally complex of all habitats surveyed. Although the vertical relief was similar to that on artificial reefs, natural rocky reefs had more cracks, crevices, and holes for fish to hide. Moreover, the algal diversity and cover was considerably greater; thus high-relief rocky reefs provided the most structurally diverse and persistent habitat.

Low-relief rocky reefs and sand/eelgrass were temporary habitats primarily utilized during the summer, coincident with summer vegetation growth. Presumably rockfishes utilize these habitats when structure and prey availability are highest and subsequently move to other more suitable habitats (Matthews In press). Although rockfish densities were low, these habitats cover considerably more area than artificial reefs or high-relief rocky reefs in Puget Sound, and thus are important to rockfish.

The highest densities of rockfishes were observed on the artificial reefs, primarily 80–200 mm quillback rockfish. Artificial reefs had high densities of 80–200 mm quillback rockfish throughout the year, although some fluctuations occurred, and high densities of large copper rockfish in the fall, winter, and spring. No other reefs surveyed had such high densities of 80–200 mm rockfishes of any species, and it is not known whether this results from higher survival of small quillback rockfish on artificial reefs. Furthermore, it is puzzling that more large quillback rockfish were not found on the artificial reefs, considering the abundance of 80–200 mm quillback rockfish. Several hypotheses could explain the low numbers of large quillback rockfish on the artificial reefs: (1) Artificial reefs are not suitable habitat for large quillback rockfish, i.e., they leave when they grow large; (2) the fish have not yet grown to the larger size; (3) some factor is preventing the fish from growing; or (4) there is a high mortality of fish once they reach the 200-mm size. I ruled out the possibility that large copper rockfish competitively excluded large quillbacks, as the two species coexist on high-relief natural reefs, although competition may be reduced at high-relief habitats if resources are not limiting. The shortage of large quillback rockfish on the artificial reefs is not depth-related since large quillbacks have been observed at similar depths in other studies (Moulton 1977, Richards 1987) and at HR1 and HR2. Again, the lack of large quillback rockfish was not due to fishing pressure: I observed low levels of fishing at both artificial reefs. Furthermore, if fishing pressure was responsible for the lack of large fish, there would be few large copper rockfish. In any case, this apparent refuge for 80–200 mm quillback rockfish should be investigated to determine if rockfish leave once they reach a certain size and eventually contribute to recreational fisheries. Although it has been well established that artificial reefs attract high densities of fish, in this case 80–200 mm quillback rockfish, there is no information that verifies whether there is adequate food or if growth or mortality is similar to that observed on natural reefs (Ambrose and Swarbrick 1989).

Year-to-year comparison

In a 4-year study of kelp-bed fishes in southern California, Ebeling et al. (1980) found little annual variation in numbers of bottom assemblages, including rockfishes. Although my study demonstrated significant seasonal changes within a habitat (artificial reefs, low relief, sand/eelgrass), when analyzed between seasons there were few differences between years, with the exception of YOY. Ebeling et al. (1980) suggested that the low annual variation in kelp-bed fish assemblages was characteristic of stable communities in predictable environments. Although more recent work (Ebeling and Laur 1988) demonstrated the dramatic effect storms can have on fish populations, Puget Sound is a relatively protected environment not subjected to open ocean waves and surge. Thus year-to-year variation in Puget Sound rockfish populations may be small.

Species comparison

Copper rockfish occurred on all habitats and can be considered a habitat generalist. Large copper rockfish were observed on all four habitats, although they left the artificial reefs in the summer and moved into shallower low-relief and sand/eelgrass areas. Buckley and Hueckel (1985) also noted a seasonal decrease of copper rockfish densities during the summer on Gedney Island artificial reef in central Puget Sound, and highest densities were noted during the fall and winter. They speculated rockfish movement was in response to prey occurrence (surfperch). Moulton (1977) speculated that copper rockfish move to deeper water during the fall in northern Puget Sound due to seasonal depth preference or prey availability. Turbulence presumably does not contribute to movement; in Puget Sound most water motion on the bottom is from currents, not surge or turbulence, and water motion is similar in the summer and winter. In the summer, copper rockfish utilized several habitats: high-relief rocky reefs, low-relief reefs, and sand/eelgrass. Their appearance on the shallower reefs during the summer and disappearance from the deeper artificial reefs is not simply a shallower depth preference in the summer; copper rockfish were observed during the summer at the high-relief reefs even at comparable artificial reef depths.

Quillback rockfish were more restricted in their distribution when compared with copper rockfish. Similarly, quillback rockfish were not as widely distributed as copper rockfish at 12 study sites in the Strait of Georgia (Richards 1987). The small quillback rockfish were seen in very high densities on the artificial reefs, but infrequently on other habitats. Large quillback rockfish were primarily seen on high-relief rocky and artificial reefs; Richards (1987) noted quillback rockfish densities were correlated with relief, and highest densities were found on complex habitats. The lack of large quillback rockfish on low-relief and sand/eelgrass areas is presumably due to their preference for high relief and complex habitats.

Brown rockfish displayed the most restricted and perplexing distribution, primarily being found on Orchard Rocks high-relief reef and the inshore low-relief reefs during the summer, and rarely observed on artificial reefs or sand/eelgrass. Brown rockfish have been observed on artificial reefs in south Puget Sound (Greg Hueckel, Wash. Dep. Fish., Olympia, WA 98504, pers. commun., summer 1988) and it is unclear why they did not inhabit the artificial reefs in central Puget Sound. Additionally, brown rockfish are relatively uncommon on rocky reefs in northern Puget Sound and the San Juan Islands (Moulton 1977). In California, brown rockfish are primarily found on sandy, low-relief areas (Matthews 1985); their different habitat use in Puget Sound could be due to local hybridization with congeners (L. Seeb, Southern Ill. Univ., Carbondale, IL 62901, pers. commun., summer 1987).

YOY were distributed differentially among all habitat types. The sand/eelgrass was a temporary YOY habitat, as YOY were observed in July and never again seen. Either the YOY left the area or died. Similarly, YOY were observed on the low-relief reefs but subsequently emigrated or suffered high mortality; their contribution to recruitment on other reefs is unknown. On the other hand, YOY were first observed on the transects on HR2 in August, although they were previously seen in July off the reef on adjacent (within 25 m) sand/*Agarum*. The numbers of YOY increased over the next few months, peaked in November, and initial settlement was followed by an increase in the 80–200 mm copper, quillback, and brown rockfishes, presumably, the result of recruits staying and growing into the larger size category. A similar pattern of YOY influx was followed by an increase in the 80–200 mm group on AR2, although two periods of YOY settlement were observed, spring and fall.

Parturition of these rockfishes reportedly occurs April through June, as most female rockfishes captured April and May near Bainbridge Island had embryos and ovaries that were in the transitional stage during the summer (DeLacy et al. 1964, Washington et al. 1979, Dygert 1986). On SCUBA surveys, I saw pregnant rockfish late April through late June. Therefore, the YOY that were observed during the summer and fall of 1987 on HR2 presumably were released between April and July, spent some unknown amount of time in pelagic regions or on some other habitat, and then settled to a demersal existence in July and August. Examinations of the otolith microstructure of eight 45–60 mm TL rockfish (M. Yoklavich, Natl. Mar. Fish. Serv., Seattle, WA 98115, pers. commun., fall 1987) that I collected 29 August 1987 on HR2 revealed approximately 120–160 growth rings. Similar growth rings have been shown to be deposited daily in black rockfish (Yoklavich and Boehlert 1987). If the rings examined on my rockfish were also daily, it would confirm that parturition occurred around April. Additionally, these fish appeared to grow quite quickly. When first observed in July and August they were approximately 45–60 mm TL and by November were 90–100 mm TL (fish were captured to verify these measurements). This scenario describes the parturition on the natural reefs which was quite different from the YOY settlement on Boeing Creek artificial reef. YOY were assumed to be primarily quillback rockfish, as YOY settlement was followed by an increase of 80–200 mm quillback rockfish. They were observed in the spring and the fall on Boeing Creek artificial reef. It is unclear when the spring recruits were released or if there are possibly two reproductive periods for quillback rockfish in Washington as noted for some California rockfishes (Wyllie Echeverria 1987). Brown rockfish sampled from one location in north-central California had two distinct seasons of larval extrusion, December and June, and Wyllie Echeverria (1987) concluded that rockfishes have a flexible reproduction system that enables individuals to adaptively respond to environmental factors. On the other hand, in my study young quillback rockfish could arrive from another source—northern Puget Sound, Strait of Juan de Fuca, or even the outer coast of Washington—causing the second pulse.

On Vancouver Island, Haldorson and Richards (1987) noted an influx of YOY (<50 mm) copper rockfish during August and September; the YOY utilized four habitat types: (1) *Nereocystis leutkeana*, (2) *Agarum* slopes, (3) eelgrass, and (4) sand. They observed the highest densities of young copper rockfish first in the bullkelp canopies. Subsequently, the young rockfish left the kelp canopy and were found on the floor of the kelp forest in September and October, coincident with fall storms and the annual decomposition of the bullkelp. After the initial association with the kelp canopy, the YOY shifted their distribution to a demersal habitat with the perennial macrophytes *Agarum* and eelgrass. Similarly, Carr (1983) first observed YOY copper rockfish in the upper canopy of giant kelp *Macrocystis pyrifera* in central California kelp beds. The YOY copper rockfish subsequently moved toward the bottom over the following weeks. Carr (1983) and Haldorson and Richards (1987) always observed YOY in close proximity to drift or attached kelp or eelgrass and suggested that young rockfishes strongly associated with plant cover to avoid predation and find food resources.

Interestingly, I never observed YOY in bullkelp canopy. The young fish were only seen on the bottom closely associated with the perennial understory macrophytes *Agarum*, *Pterygophora*, and eelgrass, or closely associated with rocks at AR2, which has little plant cover. The YOY could have spent a short period of time in the bullkelp canopy before I first saw them in my surveys or they may never use the bullkelp canopy in my study sites. Young rockfish may not be able to maintain position in the water column in areas with current.

It is not surprising that YOY rockfishes were seen in 1987, yet not in 1988. The numbers of first-year rockfish recruits reportedly vary greatly year-to-year along the coast of central and northern California (Hobson et al. 1986, Gaines and Roughgarden 1987). Studies in California have documented wide fluctuations in YOY recruitment sometimes influenced by warm-water years and changes in distribution after kelp removal (Bodkin 1988). Temperature did not appear to be a factor in the absence of YOY in 1988; bottom temperatures were similar between 1987 and 1988 (Fig. 8). In addition, few YOY were observed off eastern Vancouver Island during the same time period (summer and fall 1988) (L. Richards, Pac. Biol. Sttn., Nanaimo, B.C., Canada V9R 5K6, pers. commun., spring 1989). Apparently, copper, quillback, and brown rockfish recruitment is episodic; this has important implications to our understanding of the population dynamics and management of Puget Sound rockfishes.

The most numerous aggregations of YOY were observed on low-current reefs: HR2, AR2, and SE2. YOY were never observed on the highest current reefs, HR1 and AR1. Possibly YOY settle out on high-current reefs but lack the ability to remain on the reef and are swept away by strong current. In contrast, larvae may accumulate at sites of low current velocity. Leaman (1976) collected significantly higher numbers of *Sebastes* larvae in sheltered waters than in open, more exposed channels off the west coast of Vancouver Island. Similarly, Haldorson and Richards' (1987) observations of YOY rockfishes on eastern Vancouver Island were in low-current areas.

Experimental design

Because underwater transects are an effective means of describing large diurnally active fish populations (Brock 1954, Brock 1982), my transects were probably effective for estimating abundances of adult rockfishes, although I probably underestimated YOY rockfishes and the very dense aggregations of 80–200 mm quillback rockfish on the artificial reefs. For many size categories of the three species during most seasons, there were density differences between the two replicate sites (reefs) within each habitat type. This variability suggests there may not be a typical rocky reef or artificial reef. In most cases, though, this difference was due to variability in densities and not to different species present on the reef. For example, both AR1 and AR2 had very high densities of 80–200 mm quillback rockfish, perhaps a characteristic of artificial reefs in Puget Sound. High densities of 80–200 mm rockfishes were not observed on any other reef type, but AR2 had significantly larger densities, perhaps due to location or age of the reef.

Habitat quality

Which is the highest quality habitat? One view of habitat quality would predict that densities are directly proportional to quality; rockfish densities are highest where habitat quality is highest. This reasoning forms the basis of many current habitat assessment models in resource management (Van Horne 1983). In the absence of long-term information on growth, survival, stability, and other features of how species respond to different habitats, habitat quality is evaluated in short-term studies describing densities (Van Horne 1983). Those habitats with the highest densities will be those most important to the maintenance of that species and should ultimately be protected as critical habitat. It is important to note that densities can be misleading in designating habitat quality (Van Horne 1983). While my habitat surveys documented the highest rockfish densities on artificial reefs, the densities underwent major fluctuations. According to classic ecological theory, as density increases habitat quality declines (Svardson 1949, Fretwell 1972). If resources are limited, then at high rockfish densities, food, hiding, and resting places would be in short supply, thereby reducing growth and survival. In my study, changes in availability of resources presumably were the causes for rockfish density fluctuations. Therefore, a true measure of habitat quality should include factors other than densities, such as availability of essential resources, stability over time, survival, reproductive output, growth, and the animal's preference for that habitat. Nevertheless, copper, quillback, and brown rockfish utilized all four habitat types surveyed, and each habitat is important. But some of these habitats vary seasonally vary their suitability, and so rockfishes move to exploit alternate habitats when suitability is low (Matthews In press). Thus, for rockfishes, I would argue that high densities should not be the primary indicator of habitat quality, particularly in reference to the high ratio of small/large quillback rockfish on artificial reefs. Documenting densities of rockfishes only during a short time frame (few months) would not be representative of that habitat's importance. In addition, low-relief rocky reefs, although only important as rockfish habitat in the summer, likely represent essential summer feeding area for rockfishes. Although densities are low, this habitat type is widespread in Puget Sound. In order to protect low-relief habitats, they would obviously have to be preserved year-round, i.e.. not altered or destroyed. Thus, in terms of seasonal stability in densities, presence of all size categories, and seasonal resource availability, I suggest the following ranks for the different habitats, listed from highest to lowest: High-relief rocky reefs, low-relief reefs (important as summer feeding area and thus contribute to year-round growth), artificial reefs (pending further research and assessment), and sand/eelgrass.

Regardless of which habitat has the highest quality, the habitat types examined in this study were utilized differently by the various size groups and species. Recently, however, Hueckel et al. (1989) have suggested that artificial reefs can be used as mitigation for the loss of natural rocky-reef habitat. Mitigating the loss of natural habitats with artificial reefs uses the rationale that artificial reefs provide rocky-reef type substrate that replicates natural rocky reefs. Hueckel and Buckley (1989) reported that artificial reefs in Puget Sound replicate processes on natural reefs and provide as evidence the similarity in the number of fish and prey species present on artificial and natural reefs. My research indicated that rockfish species composition was similar (with the exception of brown rockfish) between natural and artificial reefs. However, these species utilize artificial reefs quite differently than natural reefs: Large copper rockfish leave artificial reefs during the summer, large quillback rockfish are found in small numbers, and artificial reefs are dominated by extremely high densities of small quillback rockfish, unlike any natural reef I surveyed. In fact, the artificial reefs I studied seem to represent an anomalous habitat unlike any natural habitat.

Furthermore, the difference in resource availability and habitat use may result in different birth and death rates on different habitats. Thus, the different habitats could be viewed as sources, where reproductive output exceeds deaths, or sinks, where a deficit exists (Pulliam 1988). On the superficial observation of high densities of quillback rockfishes on artificial reefs, it could be determined that the destruction of a nearby rocky reef would have little impact on rockfishes. Pulliam (1988) points out that if a habitat (e.g., artificial reef) being preserved was a sink and the one being destroyed was a source (e.g., natural rocky reef), destruction of a relatively small source habitat could then have disastrous results. For example, if a low-relief natural reef was destroyed for a development project, the loss of the productive feeding area used by artificial-reef rockfishes during the summer could result in reduced growth and less reproductive output. Again, whether or not artificial reefs provide adequate food for such high densities of rockfishes is unknown. The largest rockfish inhabiting artificial reefs were those that made use of natural habitats; their movement was confirmed in a tagging study (Matthews 1988). Thus copper rockfish may be maintained by a source habitat when they make use of kelp beds during the summer. In addition, artificial reefs are considerably smaller than natural reefs, so they would not compensate for the total loss of abundance (Ambrose and Swarbrick 1989). Thus it is premature and speculative to suggest that artificial reefs should be used as mitigation.

Summary

Habitat surveys comparing monthly densities of copper, quillback, and brown rockfishes on high-relief rocky reefs, low-relief rocky reefs, high-relief artificial reefs, and sand/eelgrass areas demonstrated strong differences in how rockfishes utilize these habitats. High-relief rocky reefs had the most consistent densities of the three species of rockfishes, mostly fish >200 mm. Low-relief rocky reefs were primarily inhabited in the summer months coincident with the summer growth of *Nereocystis leutkeana*. YOY rockfishes were also observed on low-relief reefs; however, most fish left these reefs in the fall. The highest densities of rockfishes, primarily 80–200 mm quillback rockfish (up to 420/90-m^3 transect), were observed on artificial reefs and high densities of large copper rockfish were also observed. On artificial reefs, density fluctuations were dramatic; copper rockfish densities peaked in the fall and winter and declined (to 0/transect) during the summer and quillback rockfish densities also seasonally fluctuated. Brown rockfish were rarely seen on the artificial reefs. Sand/eelgrass areas were the least utilized habitat type; only during July and August were YOY, adult copper rockfish, and brown rockfish observed on one sand/eelgrass habitat. Although all four habitats were used, natural reefs may represent source habitats that are used by and maintain rockfishes on less productive sink (artificial reef) habitats. Thus the recent use of artificial reefs as mitigation for the loss of natural reefs could have negative impacts on rockfish populations.

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Citations

Ambrose R.F., and S.L. Swarbrick
1989 Comparisons of fish assemblages on artificial and natural reefs off the coast of southern California. Bull. Mar. Sci. 44:718-733.

Barsukov, V.V.
1981 A brief review of the subfamily Sebastinae. J. Ichthyol. 21:1-26.

Bodkin, J.L.
1988 Effects of kelp forest removal on associated fish assemblages in central California. J. Exp. Mar. Biol. Ecol. 117: 227-238.

Boehlert, G.W., and M.M. Yoklavich
1984 Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. (Woods Hole) 167:354-370.

Brock, R.E.
1982 A critique of the visual census method for assessing coral reef fish populations. Bull. Mar. Sci. 32:269-276.

Brock, V.E.
1954 A preliminary report on a method of estimating reef fish populations. J. Wildl. Manage. 18:297-308.

Buckley, R.M., and G.J. Hueckel
1985 Biological processes and ecological development on an artificial reef in Puget Sound, Washington. Bull. Mar. Sci. 37:50-69.

Carr, M.H.
1983 Spatial and temporal patterns of recruitment of young-of-the-year rockfishes (Genus *Sebastes*) into a central California kelp forest. Master's thesis, San Francisco State Univ., San Francisco, CA 94132, 104 p.
1989 Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. J. Exp. Mar. Biol. Ecol. 126: 59-76.

Culver, B. N.
1987 Results from tagging black rockfish (*Sebastes melanops*) off the Washington and northern Oregon coast. *In* Proc. Int. Rockfish Symp., p. 231-240. Univ. Alaska Sea Grant Rep. 87-2, Fairbanks, Anchorage, Alaska, 99701.

Delacy, A.C., C.R. Hitz, and R.L. Dryfoos
1964 Maturation, gestation, and birth of rockfish (*Sebastodes*) for Washington and adjacent waters. Wash. Dep. Fish., Fish. Res. Pap. 2:51-57.

Dygert, P.H.
1986 Management implications of variability in reproduction and growth of commercial marine fishes. Ph.D. diss., Univ. Wash., Seattle, 98195, 275 p.

Ebeling, A.W., and D.R. Laur
1985 The influence of plant cover on surfperch abundance at an offshore temperate reef. Environ. Biol. Fish. 12:169-179.
1988 Fish populations in kelp forests without sea otters: Effects of severe storm damage and destructive sea urchin grazing. *In* Van Blaricom, G.R., and J.A. Estes (eds.), The community ecology of sea otters, p. 169-191. Ecol. Stud. 65, Springer-Verlag.

Ebeling, A.W., R.J. Larson, and W.S. Alevizon
1980a Habitat groups and island-mainland distribution of kelp-bed fishes off Santa Barbara, California. *In* Power, D.M. (ed.), Multidisciplinary symposium on the California islands, p. 404-431. Santa Barbara Mus. Nat. Hist., Santa Barbara, CA.

Ebeling, A.W., R.J. Larson, W.S. Alevizon, and R.N. Bray
1980b Annual variability of reef-fish assemblages in kelp-forests off Santa Barbara, California. Fish. Bull., U.S. 78: 361-377.

Fretwell, S.D.
1972 Populations in a seasonal environment. Princeton Univ. Press, Princeton, NJ, 217 p.

Gaines, S.D., and J. Roughgarden
1987 Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. Science (Wash. DC) 235:479-481.

Gowan, R.E.
1983 Population dynamics and exploitation rates of rockfish (*Sebastes* spp.) in central Puget Sound, Washington. Ph.D. diss., Univ. Wash., Seattle, 98195, 90 p.

Guillemot, P.J., R.J. Larson, and W.H. Lenarz
1985 Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae: *Sebastes*). Fish. Bull., U.S. 83:299-312.

Haldorson, L., and L.J. Richards
1987 Habitat use by young-of-the-year copper rockfish (*Sebastes caurinus*) in British Columbia. *In* Proc. Int. Rockfish Symp., Anchorage, Alaska, p. 129-141. Alaska Sea Grant Rep. 87-2, Fairbanks 99701.

Hart, J.L.
1973 Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.

Hobson, E.S.
1972 Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.

Hobson, E.S., P. Adams, J. Chess, D. Howard, and W. Samiere
1986 Temporal and spatial variations in the numbers of first-year juvenile rockfishes off northern California. Admin. Rep. T-86-02, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 16 p.

Hueckel, G.J., and R.M. Buckley
1989 Predicting fish species on artificial reefs using indicator biota from natural reefs. Bull. Mar. Sci. 44:873-880.

Hueckel, G.J., R.M. Buckley, and B.L. Benson
1989 Mitigating rocky habitat loss using artificial reefs. Bull. Mar. Sci. 44:913-922.

Larson, R.J.
1980 Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50:221-239.

Larson, R.J., and E.E. DeMartini
1984 Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. Fish. Bull., U.S. 82:37–55.

Laufle, J.C.
1982 Biological development and materials comparison on a Puget Sound artificial reef. Wash. Dep. Fish. Tech. Rep. 72, 183 p.

Lea, R.N.
1983 Current approaches to and problems with rockfish systematics [Abstract]. *In* Henry, F. (ed.), Proc. 1983 Groundfish Workshop, Monterey, California. Calif. Dep. Fish Game, Menlo Park, CA 94025 [unpaginated].

Leaman, B.M.
1976 The association between black rockfish (*Sebastes melanops* Girard) and beds of the giant kelp (*Macrocystis integrifolia* Bory) in Barkley Sound, British Columbia. Master's thesis, Univ. British Columbia, Vancouver, 108 p.

Love, M.S.
1980 Isolation of olive rockfish, *Sebastes serranoides*, populations off southern California. Fish. Bull., U.S. 77:975–983.

Matthews, K.R.
1985 Species similarity and movement of fishes on natural and artificial reefs in Monterey Bay, California. Bull. Mar. Sci. 37:252–270.
1988 Habitat use and movement patterns of copper, quillback, and brown rockfishes in Puget Sound, Washington. Ph.D. diss., Univ. Wash., Seattle 98195, 121 p.
In press An experimental study of habitat preferences and movement patterns of copper, quillback, and brown rockfishes. Environ. Biol. Fish.

Moulton, L.L.
1977 An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. Ph.D. diss., Univ. Wash., Seattle 98195, 181 p.

Palsson, W.A.
1988 Bottomfish catch and effort statistics from boat-based recreational fisheries in Puget Sound, 1970–1985. Wash. Dep. Fish. Prog. Rep. 261, 104 p.

Patten, B.G.
1973 Biological information on copper rockfish in Puget Sound, Washington. Trans. Am. Fish. Soc. 102:412–416.

Phillips, R.C.
1984 The ecology of eelgrass meadows in the Pacific northwest: A community profile. U.S. Fish. Wildl. Serv. FWS/OBS-84/24, 85 p.

Pulliam, H.R.
1988 Sources, sinks, and population regulation. Am. Nat. 132:652–661.

Quast, J.C.
1968 Effects of kelp harvesting on the fishes of the kelp beds. *In* North, W.J., and C.L. Hubbs (eds.), Utilization of kelp bed resources in southern California, p. 143–149. Calif. Dep. Fish Game Fish. Bull. 139.

Richards, L.J.
1987 Copper rockfish (*Sebastes caurinus*) and quillback rockfish (*Sebastes maliger*) habitat in the Strait of Georgia, British Columbia. Can. J. Zool. 65:3188–3191.

Richards, L.J., and A.J. Cass
1987 The British Columbia inshore rockfish fishery: Stock assessment and fleet dynamics of an unrestricted fishery. *In* Proc. Int. Rockfish Symp., Anchorage, Alaska, p. 299–308. Univ. Alaska Sea Grant Rep. 87-2, Fairbanks 99701.

Stephens, J.S., P.A. Morris, K.E. Zerba, and M.S. Love
1984 Factors affecting fish diversity on a temperate reef: The fish assemblage of Palos Verdes Point, 1974-1981. Environ. Biol. Fish. 11:259–275.

Svardson, G.
1949 Competition and habitat selection in birds. Oikos 1: 157–174.

U.S. Department of Commerce
1987 Tidal Current Tables 1987. Pacific Coast of North America and Asia. Natl. Ocean Serv., Natl. Oceanic Atmos. Adm., Rockville, MD 20852, 279 p.

Van Horne, B.
1983 Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893–901.

Washington, P.M., R.G. Gowan, and D.H. Ito
1979 A biological report on eight species of rockfish (*Sebastes*) from Puget Sound, WA. Proc. Rep., Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070, 50 p.

Wyllie Echeverria, T.W.
1987 Thirty-four species of California rockfishes: Maturity and seasonality of reproduction. Fish. Bull., U.S. 85:229–250.

Yoklavich, M.M., and G.W. Boehlert
1987 Daily growth increments in otoliths of juvenile black rockfish, *Sebastes melanops*: An evaluation of autoradiography as a new method of validation. Fish. Bull., U.S. 85:826–832.

Zar, J.H.
1984 Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ, 718 p.