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KELP FOREST FISH POPULATIONS IN MARINE RESERVES AND ADJACENT EXPLOITED AREAS OF CENTRAL CALIFORNIA

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Abstract. Population structure (density and size distribution) of 10 species of epibenthic kelp forest fishes was compared between three marine reserves and adjacent exploited areas in central California. We also contrasted substrate relief, algal turf cover, and kelp population density among these areas. Densities of fishes were 12-35% greater within the reserves, but this difference was not statistically significant. Habitat features explained only 4% of the variation in fish density and did not vary consistently between reserves and nonreserves. The average length of rockfish (genus Sebastes) was significantly greater in two of the three reserve sites, as was the proportion of larger fish. Population density and size differences combined to produce substantially greater biomass and, therefore, greater reproductive potential per unit of area within the reserves. The magnitude of these effects seems to be influenced by the reserve's age. Our findings demonstrate that current levels of fishing pressure influence kelp forest rockfish populations and suggest that this effect is widespread in central California. Existing marine reserves in central California kelp forests may help sustain exploited populations both through adult emigration and larval pool augmentation. The magnitude of these effects remains uncertain, however, because the spatial scale of both larval and adult dispersal relative to the size of existing reserves is unknown.

Key words: kelp forests; marine reserves; reproductive potential; rockfish; Sebastes.

INTRODUCTION

Marine resources worldwide are showing signs of degradation (Dayton et al. 1995, Botsford et al. 1997, Lauck et al. 1998, Pauly et al. 1998), and rockfish (Scorpaenidae; Sebastes) are no exception (Love et al. 1998, Ralston 1998). Rockfish are an important component of commercial and recreational fisheries in western North America (40% of the revenue from U.S. commercial groundfish landings in 1996, totaling >32 million dollars, Pacific Fishery Management Council 1998, Lea 1992). This diverse group of fishes (59 species, Yoklavich 1998) is targeted by year-round midwater and demersal fisheries in both deep offshore waters and nearshore reef environments. The fishery has changed dramatically since its inception in the late 1800's (Pacific Fishery Management Council 1998). California's commercial landings peaked in 1983 at \sim 24000 metric tons but have since declined (Dugan and Davis 1993, Yoklavich 1998). Whether these declining trends are from overfishing, long-term change in oceanographic conditions (Love et al. 1998), or perhaps some other factor is unclear. What is clear is that rockfish stocks are in jeopardy of overexploitation (Gunderson 1997, Ralston 1998, Murray et al. 1999).

Life history traits of most rockfish species make them vulnerable to overfishing (Wyllie Echeverria 1987, Leaman 1991, Gunderson 1997). These include stochastic recruitment (Moser and Boehlert 1991, Ralston and Howard 1995, Love et al. 1998), late maturation (Wyllie Echeverria 1987), slow growth (Love et al. 1990, Beverton 1992), limited movement from resident reef areas (Miller and Geibel 1973, Larson 1980), and multispecies aggregations (Leaman 1991). Their vulnerability is becoming increasingly apparent through reports of reductions in biomass (Karpov 1995, Pacific Fishery Management Council 1995, Ralston 1998), size (Ralston et. al 1990), and landings (Dugan and Davis 1993, Pacific Fishery Management Council 1998). Inshore rockfishes are of particular concern, as declines and closures of other fisheries (e.g., restrictions on California's inshore setnet fishery, declines in salmon and Alaska's rockfish fisheries; P. Reilly, California Department of Fish and Game, personal communication; Pacific Fishery Management Council 1993) and gear shifts (especially the growing live fish fishery) have increased fishing pressure in shallow waters (Hardy 1996, Love and Johnson 1999, Murray et al. 1999). Fishing of nearshore rockfish stocks is increasing while stock assessments and knowledge of fishery effects are unknown for most species (National Marine Fisheries Service 1997). Clearly, there is a need

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for more information on rockfish stocks and evaluation of management practices.

In response to the increasing evidence that management has failed to achieve sustainability in this and many other fisheries (Dayton et al. 1995, Botsford et al. 1997, Ralston 1998), there is growing interest in the use of no-take areas (marine reserves) as a fisheries management tool (Bohnsack 1998, Castilla and Fernandez 1998, Dayton 1998). Marine reserves may serve as buffers against catastrophic declines caused by the synergistic interaction between exploitation and environmental extremes (Bohnsack 1993), as well as protect against the inherent risk of uncertainty in fisheries management (Bohnsack 1993, Lauck et al. 1998). Additionally, they may aid in sustaining and possibly enhancing stocks (Murray et al. 1999). The use of marine reserves in the management strategy for rockfish in particular has begun to receive serious attention (Yoklavich 1998, Lea et al. 1999).

Beneficial effects of marine reserves on fish and invertebrate populations have been demonstrated in numerous studies. These effects include increased density (Alcala 1988, Bennett and Attwood 1991, Buxton and Smale 1989, Russ and Alcala 1989, McClanahan and Shafir 1990, Polunin and Roberts 1993, Grigg 1994, Jennings et al. 1994, McClanahan 1994, Watson and Ormond 1994, McClanahan and Kaunda-Arara 1996, Stoner and Ray 1996), and increased individual size and age in targeted populations (Bell 1983, Mc-Clanahan and Muthiga 1988, Cole et al. 1990, Bennett and Attwood 1991, Buxton 1993, Roberts 1995, Rakitan and Kramer 1996, Sala and Zabala 1996). Additionally, some reserves have been shown to enhance habitat quality (e.g., recovery of corals) (Roberts and Polunin 1993, McClanahan 1997a), species diversity (McClanahan and Muthiga 1988, Cole et al. 1990, Jennings et al. 1994, Harmelin et al. 1995, McClanahan and Obura 1996, Russ and Alcala 1996, McClanahan 1997b), and to increase community stability (Castilla and Durán 1985, Roberts and Polunin 1993, Dayton et al. 1995). Reserve effects may extend beyond reserve boundaries through spillover of adults and/or larvae to fishing grounds. Adult fish spillover is likely the cause of increased yields or catch per unit effort in areas adjacent to reserves (Russ and Alcala 1989, Attwood and Bennett 1994, Holland et al. 1996, McClanahan and Kaunda-Arara 1996, Castilla and Fernandez 1998).

There are 103 marine protected areas along the California coast, only 11 of which receive protection from all take (McArdle 1997). Despite the lack of clearly stated management objectives in many marine reserves (Björklund 1974, McArdle 1997), the public and resource users often view total no-take areas as a means to augment harvested populations. Unfortunately, most of California's marine protected areas lack baseline biological information, without which their effects cannot be evaluated. Obtaining this information is crucial if marine reserves are truly going to be incorporated into fisheries management. In addition, regardless of whether the reserves are used for fisheries management, information obtained from unexploited populations may improve population parameter estimates for fished populations (Smith et al. 1998, Murray et al. 1999).

Our goal was to assess the effect of marine reserves on populations of exploited fish species in central California kelp forests. We did this by contrasting three existing marine reserves with nearby areas in which fishing was permitted. This approach has been used elsewhere to evaluate the influence of fishing on reef fish populations (see, for example, Buxton and Smale 1989, Cole et al. 1990, Grigg 1994, McClanahan 1994), although relatively few of these have been conducted in cold-temperate regions (Bohnsack 1998) (for coldtemperate examples, see-South Africa: Buxton and Smale 1989, Bennett and Attwood 1991, Buxton 1993, Attwood and Bennett 1994; Chile: Castilla and Durán 1985, Castilla 1996, Castilla and Fernandez 1998; USA: Palsson and Pacunksi 1995, Rogers-Bennett et al. 1995, Palsson 1998), and only three other studies have considered kelp forest fishes (Cole et al. 1990, Palsson and Pacunski 1995, Palsson 1998). Cold water/ kelp forest systems differ from tropical reefs in numerous ways, several of which may influence their susceptibility to fishing. Compared with coral reefs, kelp forests are more productive (Duggins et al. 1989), have a lower fish species diversity (Ebeling and Hixon 1991), and support fish faunas with higher overall trophic status because of the paucity of herbivorous species (Gaines and Lubchenco 1982), at least in the northern hemisphere (Choat 1982).

MATERIALS AND METHODS

Field research was done from 1994 through 1996 in or near three marine reserves (referred to hereafter as areas; Fig. 1) within the Monterey Bay National Marine Sanctuary: Hopkins Marine Life Refuge (all fishing prohibited since 1984), Point Lobos State and Ecological Reserve (designated as a State Reserve in 1963 which prohibited invertebrate collection but allowed commercial and recreational fishing, all fishing prohibited since 1973), and Big Creek Marine Ecological Reserve (all fishing prohibited since January 1994). Nonreserve areas consisted of at least two sites nearby each reserve (Table 1). All sampling was done in habitats with a giant kelp (*Macrocystis pyrifera*) surface canopy at \sim 14 m depth over rocky substrates with moderate rock relief.

Species

We focused on fishes that are both common in central California kelp forests and exploited by commercial and recreational fisheries. This included six rockfish species; *Sebastes atrovirens* (kelp rockfish), *S. carnatus* (gopher rockfish), *S. caurinus* (copper rockfish), *S. chrysomelas* (black and yellow rockfish), *S. nebulosus* (china rockfish), and *S. miniatus* (vermilion rockfish);



FIG. 1. Location of study areas. Nonreserve sites (listed in Table 1) are marked as dots; reserves are shaded.

and four others; Ophiodon elongatus (lingcod), Hexagrammos decagrammus, (kelp greenling), Semicossyphus pulcher (sheephead), and Scorpaenichthys marmoratus (cabezon). Population analyses focused on the rockfishes. Young-of-the-year (YOY) were not surveyed as their numbers are seasonal, they utilize different habitats than adults (often recruiting into the giant kelp canopy; Carr 1989), and are difficult to distinguish to species in the field.

A hierarchical cluster was generated in order to compare fish species assemblages among areas. Dissimilarities were computed using 1 minus the Pearson product-moment correlation coefficient (Systat). The same method was used to cluster areas based upon habitat variables. In combination, these analyses were used to evaluate the relative importance of geographic location, reserve versus nonreserve status, and habitat structure on fish species composition.

Fish counts

The density of targeted fish species was estimated from fish counts by scuba divers within randomly placed, 50×4 m transects. All transects were located from randomly selected origins and compass bearings. Sampling was terminated if large sand patches or extreme changes in depth/contour were encountered (minimum transect length was 20 m). Two divers simultaneously counted the number of fish encountered in a swath 2 m wide and 1 m above the bottom on either side of the transect. The counts were summed to provide a single 4 m wide swath count for each transect. Visibility was estimated by determining the maximum distance at which one diver could count the fingers on the other diver's hand when held above their head in the water. Fish counts were conducted only when this distance was >3 m. Between 6 and 30 transects were sampled at each site. Sample sizes were unequal due to extreme swell and surge and low visibility at some sites during the study period, which limited our ability to accurately and safely conduct the surveys.

Habitat surveys

Habitat surveys were conducted to (1) determine the degree of similarity among sites in topography, turf algal species composition and abundance, and kelp density; and (2) discern whether habitat variation influenced fish populations. Algal abundance and cover were measured because algae provide recruitment habitat for rockfish, shelter fishes from predation, and provide a substrate for prey (Love et al. 1991).

Divers counting fish were followed along the transect by two habitat surveyors. One surveyor measured the percent cover of turf algae by placing a 1-m² quadrat at a randomly chosen distance along each 5-m segment of the transect. Turf algae were categorized as fleshy reds (e.g., Gigartina spp., Gelidium robustum, Rhodymenia californica), articulated corallines (Corallina spp., Bosiella spp., Calliarthron spp.), encrusting corallines (Lithothamnium spp. and Lithophyllum spp.), and epibenthic browns (Dictyopteris spp., Dictyoneurum californicum, Desmarestia ligulata, Cystoseira osmundacea), and the percent cover for each category was visually estimated (Dethier et al. 1983). The second diver counted sporophytes >1 m high of giant kelp (Macrocystis pyrifera) and other stipitate brown algae (Laminaria spp., Pterygophora californica, Eisenia arborea) in a swath 1 m to either side of the transect. The second diver also classified the substrate in each 5 m segment as being predominately sand, cobble, flat rock, low boulders (<1 m high), medium boulders (1-3 m high), or pinnacles (>3 m high). Bottom depth was recorded at 5-m intervals along the transect. The relationship between fish density and each of the habitat factors was evaluated using a stepwise linear regression.

Fish sizes

Total length of individual fishes was estimated in situ to the nearest centimeter with a diver-held Plexiglas ruler mounted perpendicularly at the end of a 1m long rod (the rod and flexible ruler allowed divers to measure fish in crevices). Transects to measure fish sizes were conducted in the same areas as fish counts, but on different days in order to not bias either the count or size data. Two divers swam a square course

		Location		
Area	Site	(mean depth, range)		
Hopkins Marine Life Refuge	"Lead line" (HMLR-LD)	Midreserve (off Bird Rocks) (9.1 m, 5.5–12.1 m)		
	Hopkins East (HMLR-E)	At the eastern edge of the reserve (103 m. 9.7–11.8 m)		
	Hopkins West (HMLR-W)	Western-facing side of the reserve (10 m, 8.8–12.1 m)		
Hopkins: adjacent nonreserve	Monterey Bay Aquarium (MBA)	Reef in front of the Monterey Bay Aquarium (0.2 km from the eastern reserve boundary)		
	Macabe Beach	(10.6 m, 7.6–12.1 m) SW off Macabe Beach (0.9 km from the easterr reserve boundary) (11.2 m, 7.3–13.2 m)		
	Green Gables	In front of the Green Gables B&B (0.6 km from western reserve boundary) (12 1 m 9 1–130 m)		
Pt Lobos Marine Reserve	Cypress Cove	Toward the western point of the Reserve $(12 \text{ m } 85-185 \text{ m})$		
	Whalers Cove	Near the mouth of Whalers Cove $(10.6 - 17.0 \text{ m})$		
Pt Lobos: adjacent nonreserve	Mono Lobo	NE of Whalers Cove (0.2 km from the reserve boundary)		
	South Monastery	(12.7 m, 12.7-18.2 m) Off the southern end of Monastery Beach (0.5 km from the reserve boundary) (13.6 m, 7.0, 17.0 m)		
Big Creek Marine Ecological Reserve	Big Creek Cove	Off the main beach $(13.9 \text{ m}, 11.8 - 15.2 \text{ m})$		
Leological Reserve	Square Black Rock	1.6 km north of the cove (15.2 m, $8.2-20.9$ m)		
Big Creek: adjacent nonreserve	Slate Rock	Off Esalen (3.2 km from the northern reserve boundary)		
	Vicente Creek	(13.6 m, 12.1–23.3 m) First creek south of Big Creek (1.2 km from the southern reserve boundary) (12.6 m, 10.2, 21.2 m)		
	Lopez Point	South of Vicente Creek (3.2 km from the sout ern reserve boundary) (191 m, 17.0–21.2 m)		

TABLE 1. List of sites for each reserve and adjacent nonreserve.

starting at the boat's anchor, measuring every targeted fish species that was encountered within 1 m of the sea floor. The accuracy of this method was evaluated by collecting some of the fish with a pole spear in non-reserve areas after they had been measured in situ. This was done for 32 individual fish of three species (*S. carnatus, S. chrysomelas,* and *S. atrovirens*), ranging in total length from 14 to 32 cm. In situ measurements of fish length ranged from <1 cm to >2 cm actual length (average difference was + 0.13 cm \pm 0.98 sp).

Fish lengths were compared both by individual species and all rockfish species combined. Mean lengths were calculated for each site and compared with a ttest between each reserve/nonreserve pair. Differences in fish size frequency distributions between adjacent reserve/nonreserve sites were evaluated with a Kolmogorov-Smirnov two-sample test (SYSTAT, Evanston, Illinois, USA). The resulting P values were pooled to obtain a single experiment-wide value for the reserve/nonreserve comparison (Rice 1990).

Fish biomass and reproductive potential

Total length (TL) measurements were converted to standard lengths (SL) using SL/TL ratios provided for

each species by Lea et al. (1999). A mass-standard length regression, based on >500 individuals of *S. atrovirens* and *S. chrysomelas* collected near Monterey, California between 1984 and 1986 (R. J. Larson, *personal communication*), was then used to convert standard length to biomass. Although other *Sebastes* species in our study areas may have similar mass-length relationships due to their similar body forms, we did not extrapolate the biomass estimates to these species as small differences in length/weight relationships can translate into large differences in biomass for equal numbers of fish. Fish biomass per unit area for each site was calculated by summing the product of mass for each size class of fish, the proportion of fish in the corresponding size class, and fish density.

Length-specific fecundity (LSF) was calculated for *S. atrovirens* and *S. chrysomelas* using relationships with standard length (SL) provided by Romero (1988) and Zaitlin (1986) respectively (*S. atrovirens*: LSF = $(2.1 \times 10^{-5})(\text{SL}^{4.134})$, $r^2 = 0.788$; *S. chrysomelas*: LSF = $(1.36 \times 10^{-8})(\text{SL}^{5.59})$, $r^2 = 0.92$). We use the term "reproductive potential" to describe the number of eggs produced per area of habitat by a population. Re-



FIG. 2. Substrate comparisons between reserve and non-reserve areas.

productive potential was estimated for each species and site by summing the product of the fecundity for each size class, the proportion of fish measured in the corresponding size class, and fish density. For this computation, fish density was determined by dividing the fish counts by two, assuming that rockfish have a 50: 50 sex ratio (as there is no evidence to the contrary for inshore rockfishes).

RESULTS

Habitat analyses

The predominant substrate types within both Hopkins Reserve and the adjacent nonreserve sites were low and medium profile granite outcrops and boulders surrounded by sand plains (Fig. 2a). Hopkins Reserve had slightly higher relief, with more medium-sized boulders and pinnacles than the nonreserve site, which was predominated by low boulders and sand, causing the nonreserve site to appear slightly deeper than the reserve site (11.3 m \pm 1.2 sD vs. 9.2 m \pm 1.9 sD). The Pt. Lobos Reserve was also characterized by a somewhat higher relief than the nonreserve site (Fig. 2b) although the average depths of these two sites were nearly identical (12.5 m \pm 1.3 sD and 12.2 m \pm 2.8 sD, respectively). At Big Creek, the reserve site had lower relief and was shallower (14.4 m \pm 2.7 sD vs. 16.0 m \pm 2.8 sD) than the nonreserve site (Fig. 2c).

Frequency distributions of substrate types was tested for each reserve vs. nonreserve area with a Kolmogorov-Smirnov two-sample test, and no significant differences were found between sites (Hopkins P = 0.15, Pt. Lobos P = 0.26, Big Creek P = 0.36). Depth did not differ significantly among sites (two way ANOVA, $F_{1,2} = 0.49$, P = 0.56).

Frequency distributions of percent cover for articulated coralline, encrusting coralline, brown, and foliose red algae varied considerably between each reserve/nonreserve pair (Fig. 3). *G* tests showed that 8 of 12 possible pairwise comparisons (3 areas \times 4 algal categories) between reserve and nonreserve sites differed significantly. However, there were no consistent trends for any algal class between reserve and nonreserve areas (Fig. 3). Neither giant kelp (ANOVA, $F_{1,2}$ = 1.24, *P* = 0.38) nor epibenthic stipitate kelp (AN-OVA, $F_{1,2}$ = 3.99, *P* = 0.18) densities differed significantly between reserve and nonreserve sites (Table 2). All data conformed with the assumptions of ANOVA.

A multiple regression showed significant correla-



FIG. 3. Average percent cover of turf algae in reserve and nonreserve areas for each of four categories: *P < 0.05, **P < 0.01, ***P < 0.001.

Canopy Understory Area Reserve Nonreserve Reserve Nonreserve 1.6 ± 1.27 1.6 ± 0.71 1.2 ± 1.91 0.4 ± 0.62 Hopkins 1.7 ± 1.77 Pt. Lobos 1.3 ± 0.78 5.3 ± 1.39 2.4 + 2.11 3.6 ± 1.82 4.9 ± 3.87 Big Creek 0.7 ± 0.60 4.4 ± 3.45

TABLE 2. Mean counts (individuals/10 m²; \pm 1 sD) of canopy (*Macrocystis pyrifera*) and understory (*Laminaria* spp., *Pterygophora californica, Eisenia arborea*) kelps.

tions between articulated coralline algae (P = 0.01), brown algal ground cover (P = 0.03), and stipitate kelps (P = 0.009) and rockfish density. Collectively however, these factors described only 4% of the variation in fish density ($r^2 = 0.041$). Overall, the measured habitat variables clustered most closely by area (Fig. 4a).

Fish species composition

Fish species composition differed somewhat among the three study areas, due to the absence or very low density of certain species at some sites, but this did not appear to be due to reserve status (Fig. 5). Cluster analysis indicated that species composition was most similar between each reserve/non-reserve pair (Fig. 4b). At Pt. Lobos and Big Creek, *S. carnatus* was the most common species whereas *S. atrovirens* was the most common species at Hopkins. *S. nebulosus* was rare, found only in the Big Creek sites and the nonreserve site at Pt. Lobos. *Semicossyphus pulcher* (a labrid fish near the northern end of its geographic range in central California: Miller and Lea 1972) occurred at Big Creek, was rare at Pt. Lobos, and was absent from our samples at Hopkins.

Fish density

There were 12–35% more fish within the reserve vs. nonreserve sites (Fig. 6), but these results were not statistically significant (two-way blocked ANOVA, $F_{1,2}$ = 12.751, P = 0.07). It should be noted, however, that the power of this test is very low (1 – β < 0.20 for effect size of 0.12, 0.41 for d = 0.25). None of the individual species densities differed significantly be-

tween reserve and nonreserve sites (ANOVA results and densities listed in Table 3). The data met all assumptions for ANOVA.

Population structure

Size-frequencies were combined within sites for those rockfish species having similar maximum sizes (i.e., S. carnatus, S. chrysomelas, S. atrovirens, S. caurinus; Fig. 7). For the two reserve sites protected the longest (Hopkins, 12 yr; Pt. Lobos, 23 yr), average lengths were significantly greater within the reserves (Hopkins: t = 9.29, df = 390, P < 0.001; Pt. Lobos: t = 7.10, df = 191, P < 0.001). Mean lengths at Big Creek (protected for 1 yr) did not differ significantly (t = 0.51, df = 328, P = 0.304). Kolmogorov-Smirnov two sample tests for each reserve/nonreserve comparison also showed significantly different length frequency distributions (i.e., population structures) at Hopkins (P < 0.001) and Pt. Lobos (P < 0.001), but not Big Creek (P = 0.99). The similar size-frequency distributions between reserve and nonreserve areas at Big Creek is not surprising given that our study was conducted immediately after the reserve in that area was established. Pooled Kolmogorov-Smirnov tests resulted in a significant difference between reserves and nonreserves overall (P = 0.0002).

Length distributions were also compared between reserves and nonreserves with Kolmogorov-Smirnov tests for each species in which we had at least 10 measurements from both paired sites. Differences were detected for all species tested at Hopkins and Pt. Lobos (Hopkins: S. chrysomelas P < 0.001, S. atrovirens P



FIG. 4. Cluster diagrams based on (a) habitat variables and (b) species composition. Dissimilarity is computed as 1 minus the Pearson product-moment correlation coefficient. (H = Hopkins, L = Pt. Lobos, B = Big Creek, I = Inside reserve, O = Outside reserve.)



FIG. 5. Species composition of surveyed fish species at each reserve and nonreserve site.

< 0.001; Lobos: S. chrysomelas P = 0.002, S. atrovirens P = 0.002, S. carnatus P = 0.001) whereas no differences were detected at Big Creek (S. atrovirens P = 0.373, S. carnatus P = 0.059).

The population of nonreserve fish at Hopkins and Pt. Lobos was dominated by small size classes, whereas at Big Creek the proportions within each size class were similar between reserve and nonreserve sites (Fig. 7). This pattern held for each of the common rockfish species.

Biomass

Biomass density (g fish/10 m²) estimates for S. atrovirens and S. chrysomelas at both Hopkins and Pt. Lobos were $>2 \times$ higher in the reserve than nonreserve



FIG. 6. Fish densities (mean + 1 SE) in reserve and nonreserve areas for all species combined (n = number of transects per area).

sites while at Big Creek there was no discernible difference between the reserve and nonreserve sites (Fig. 8).

Reproductive potential

While the length-fecundity equations are power functions typical of mass-length allometries (Zaitlin 1986, Romero 1988), they diverge considerably between *S. atrovirens* and *S. chrysomelas* for fish >20 cm standard length. Based on these length-fecundity relationships and size frequency distributions, estimated reproductive output for both species was greater in the reserve than the nonreserve sites at Hopkins and Pt. Lobos, but similar at Big Creek (Fig. 9). The comparatively low estimates for Big Creek result from the

general lack of larger individuals in both reserve and nonreserve sites.

DISCUSSION

A difficulty with large-scale comparisons of the sort we used is in distinguishing between habitat variation and reserve effects. While our data revealed some habitat differences between specific reserve and nonreserve sites, these were generally inconsistent among areas. Thus, if habitat differences did influence fish abundance, this influence would have been manifested as increased experimental error rather than by confounding the treatments.

We found fish species composition to cluster more strongly with geographical area than reserve status, thus differing from other reports of distinct shifts in community structure on exploited tropical reefs (Koslow et al. 1988, Roberts and Polunin 1991, McClanahan 1994, Wantiez et al. 1997). The reason for this difference is uncertain. Fish diversity in cold-temperate regions is relatively low, with few herbivorous species (only one resident in this area: Girella nigricans). In contrast, tropical reef fishes are characterized by greater trophic complexity, with numerous herbivore species. The lack of species differences between reserve and nonreserve areas in central California may be related to this difference or any number of other factors, including temperate/tropical differences in productivity, fishing intensity, or the strength of top-down forces.

The small differences in density between reserve and nonreserve sites may indeed indicate a relatively small impact of fishing on kelp forest fish populations. However, this is not necessarily the case. The lack of a

TABLE 3. Density of each fish species (individuals/10 m²; \pm 1 sD).

	нор	KINS	Pt. I	Pt. Lobos Big Creek		леек
Fish species	Reserve	Nonreserve	Reserve	Nonreserve	Reserve	Nonreserve
$\overline{Sebastes \ carnatus} \\ (F_{1,2} = 3.40, P = 0.21)$	0.12 ± 0.17	0.04 ± 0.06	0.28 ± 0.26	0.28 ± 0.22	0.33 ± 0.27	0.22 ± 0.23
S. chrysomelas $(F_{1,2} = 0.01, P = 0.93)$	0.13 ± 0.13	$0.08~\pm~0.12$	0.17 ± 0.18	0.17 ± 0.13	$0.05~\pm~0.10$	0.10 ± 0.23
S. caurinus ($F_{1,2} = 2.87, P = 0.23$)	0.02 ± 0.04	0	0.04 ± 0.07	$0.04~\pm~0.09$	$0.03~\pm~0.05$	0.01 ± 0.03
S. atrovirens ($F_{1,2} = 8.99, P = 0.10$)	0.33 ± 0.41	0.23 ± 0.30	0.24 ± 0.15	0.18 ± 0.30	0.20 ± 0.30	0.17 ± 0.15
S. miniatus ($F_{1,2} = 0.34, P = 0.62$)	0	0	0.02 ± 0.03	0	0	$0.04~\pm~0.04$
S. nebulosus ($F_{1,2} = 0.13, P = 0.75$)	0	0	0	0.003 ± 0.01	0.004 ± 0.01	0.002 ± 0.01
Scorpaenichtys marmoratus ($F_{1,2} = 0.20, P = 0.70$)	0.03 ± 0.04	$0.03~\pm~0.04$	$0.02~\pm~0.03$	0.03 ± 0.04	$0.02~\pm~0.04$	0.01 ± 0.03
Semicossyphus pulcher ($F_{1,2} = 1.25, P = 0.38$)	0	0	0.01 ± 0.02	0	$0.09~\pm~0.19$	0.04 ± 0.07
Ophiodon elongatus ($F_{1,2} = 2.60, P = 0.25$)	0.01 ± 0.02	0.01 ± 0.02	0.04 ± 0.06	0.01 ± 0.02	$0.02~\pm~0.05$	0.02 ± 0.02
Hexagrammos decagrammus $(F_{1,2} = 2.18, P = 0.28)$	0.04 ± 0.06	0.05 ± 0.06	0.04 ± 0.06	0.02 ± 0.03	$0.07~\pm~0.07$	$0.04~\pm~0.06$

Note: The F statistics below each fish species are for overall reserve effects.



FIG. 7. Length frequency distributions of rockfish species combined (*S. atrovirens, S. chrysomelas, S. carnatus*, and *S. caurinus*) in the reserve and nonreserve areas at Hopkins, Pt. Lobos, and Big Creek.

significant difference in fish density estimates between reserve and nonreserve sites is surprising, given the high fishing intensity in central California kelp forests (Karpov 1995) and the fairly long duration of reserve status for two of the sites. There are several possible explanations for this apparent enigma, including (1) low power of detection, (2) an inverse size-density relation among the fishes, (3) reserves that are too small to allow buildup of biomass, (4) high spillover rates, (5) limited recovery since the time of protection, and (6) poaching. We discuss each of these possibilities below.

Lack of power

Similar findings have been obtained from studies of tropical reef fishes, i.e., higher but statistically nonsignificant fish densities in reserves compared to nonreserves (Buxton and Smale 1989, Cole et al. 1990,





FIG. 8. Average biomass (+1 sE) per unit area (10 m^2) for *S. atrovirens* and *S. chrysomelas* in reserve and nonreserve areas.

García-Rubies and Zabala 1990, Roberts 1995), indicating a signal from the effects of fishing that is intrinsically difficult to demonstrate statistically. These analyses all lack statistical power due to both small sample size (few reserves) and high variation among sample units, neither of which have obvious solutions. Differences, therefore, may not be rigorously detectable except in extreme cases (Russ and Alcala 1989).

The best way to reliably assess the effects of fishing (or prohibition thereof) is with a BACI design (Underwood 1992; e.g., Wantiez et al. 1997). Unfortunately, marine reserves are typically established without monitoring programs or baseline data, thus making BACI analysis impossible. This was the case with our study.

Reserves too small

When home range size is large relative to reserve size, a species' probability of extinction within a reserve or protected area may be high (Woodroffe and Ginsberg 1998). Furthermore, if their normal movements frequently take individuals beyond a reserve boundary, stock increases within the reserve are unlikely. Nonetheless, small marine reserves in other areas have been shown to support elevated fish biomass

FIG. 9. Estimated reproductive potential (mean + 1 sE) for *S. atrovirens* and *S. chrysomelas* in reserve and nonreserve areas.

(Russ and Alcala 1989, 1996, Polunin and Roberts 1993, Roberts 1995, Jennings et al. 1996, Palsson 1998), suggesting that small reserve size does not necessarily preclude population effects. While biomass may increase in a small reserve, density may not increase appreciably (Roberts and Hawkins 1997), particularly if larger fishes limit resources or prey on smaller individuals. Small or isolated reserves also are more likely to be dependent upon external sources of larvae, making them vulnerable to recruitment overfishing in heavily fished areas (DeMartini 1993, Jennings et al. 1996, Roberts 1997, Carr and Raimondi 1998). Reserve size may be important if the goal is to sustain or enhance fished stocks through larval dispersal.

Fewer but bigger fish

Increased sizes of fish within a reserve may depress overall abundance if the larger fish are territorial and thus require more space per individual. García-Rubies and Zabala (1990) reported lower density and larger size of *Serranus cabrilla* inside compared with outside reserves in the Medes Islands. They attributed the lower density to habitat monopolization by larger, territorial individuals. Larson (1980) found that two of the rockfish species included in our study, *S. carnatus* and *S. chrysomelas*, aggressively defended distinct shelter holes and home ranges against congeners as well as other fish species. Although this behavior does not necessarily lead to exclusive use of the defended area (Larson 1980), it may limit the number of rockfish inhabiting a reef, particularly as the size of residents increases.

Spillover

Fish densities adjacent to reserves may be increased by adult dispersion or by a large and highly dispersed pool of larvae that is enhanced by reserve productionboth purported benefits of marine reserves (Roberts and Polunin 1993, Roberts 1995). Several studies have shown increased fish abundance in exploited areas nearby marine reserves, a phenomenon attributed to adult spillover from the reserves (Polunin and Roberts 1993, Attwood and Bennett 1994, Russ and Alcala 1996, Wantiez et al. 1997). This effect also may decrease rockfish density differences between exploited and protected areas. While there is some evidence that rockfish move from areas of high to areas of low population density (Matthews 1985), they also have been shown to possess very limited ranges (Miller and Geibel 1973, Larson 1980). Additionally, the fact that population size-frequencies differed significantly between reserve and nonreserve areas at both Pt. Lobos and Hopkins indicates either limited dispersal of larger fish out of the reserves, or that larger fish that disperse beyond the reserve boundaries are quickly taken. It is possible that a critical density of fish may need to build up within the reserves before spillover occurs on a measurable scale (Russ and Alcala 1996). The degree to which rockfish disperse in response to local congener density is unknown.

Recovery time

Density and biomass may be slow to recover from fishing pressure (Holland and Brazee 1996, Russ and Alcala 1996, Gunderson 1997, McClanahan 1997a). Russ and Alcala (1996) demonstrate that a density difference may not occur for four to six years. This may be particularly so, or longer, for rockfish, as they are typically long lived, slow growing, and late to mature (Love et al. 1990, Leaman 1991). The species included in this study are among the shortest-lived rockfish, with maximum lifespans of 25 yr, maturing at 4-10 yr (Larson 1980, Love et al. 1990, Lea et al. 1999). Additionally, recovery may be limited by stochasticity in recruitment patterns, with single strong year classes becoming a large component of the stock biomass (e.g., Ralston and Pearson 1997). Although we have not attempted to model population growth, a cursory estimate of recovery time based upon growth curves (Love and Johnson 1999) suggests that it would take 2-5 yr for fishes outside reserves to reach the maximum lengths seen inside reserves. Therefore, the comparatively long times both Hopkins and Pt. Lobos have been closed to fishing (12 and 23 yr, respectively) seem adequate for larger increases than the 12–35% indicated by our data.

Poaching

The fact that there is no significant difference in density, given the duration of these closures relative to the longevity of these fishes, may reflect continued mortality from fishing. Poaching undoubtedly occurs in central California. Interviews with reserve managers and wardens affirmed this. Thirteen incidents of poaching were recorded within the Big Creek reserve from January 1994 to October 1996 (J. Smiley, personal communication). Citations for illegal fishing in the Hopkins reserve have been issued at rates of about 15-20/yr (Warden Fitzsimmons, California Department of Fish and Game, personal communication) and one per week at Pt. Lobos (J. Loomis, personal communication). The poaching pressure within these reserves is very likely to considerably surpass the incidental observations, so mortality from fishing may be high. We cannot determine how much of a density difference would exist if these areas were truly no-take, but it might be substantial. Other studies report fish density increases in marine protected areas following the institution of more stringent regulations (Russ and Alcala 1994, Watson and Ormond 1994, Jennings et al. 1996). Thus, poaching may have substantially influenced our findings as well as those from other marine reserve studies (Murray 1998, Murray et al. 1999). Without insuring more complete protection, marine reserves are unlikely to fully benefit fisheries management.

Size structure

The length-frequency data from our study provide additional and statistically stronger support for rockfish population differences between protected and unprotected kelp forest sites. Increased fish sizes within reserves have been demonstrated in many other studies (Dufor et al. 1995, see Roberts and Polunin 1991 for review). Thus, size distributions and biomass may reveal more about reserve effects than density alone.

An intriguing feature of the length-frequency data from our study is the near absence of small individuals within the Hopkins and Pt. Lobos reserves. Other studies show similar patterns (García-Rubies and Zabala 1990, Dufor et al. 1995, Wantiez et al. 1997). There are several possible explanations: lower recruitment to reserve areas compared to adjacent nonreserves, increased predation pressure (Roberts and Polunin 1991), or increased postsettlement movement in response to competition for resources. It seems unlikely that differences in larval recruitment explain the differences in our study. The close proximity of sites, similarities in habitat between reserve and nonreserve areas (particularly kelp abundance), and observations of large numbers of young-of-the-year rockfish within the kelp

92 83

89

100

100

0

0

38

0

0

100

25, 10-30

6, 13-26

100, 10-33

42, 17-34

39, 16-37

5, 25-30

3. 19-26

8, 28-43

none

1,24

none

none

2, 30-35

4.40 - 48

S. atrovirens

S. caurinus

S. nebulosus

S. miniatus

Reserve Nonreserve Percent-Percent-Size (and age) at n, Size range n, Size range age age Fish species 50% maturity Area (cm)mature mature (cm)Hopkins 15, 10-30 17 (4 yr) 28, 15-35 96 87 S. carnatus Pt. Lobos 18, 16-37 94 55, 10-35 82 Big Creek 123, 9-35 93 85, 9-32 94 Hopkins 44, 18-36 100 29, 11-31 88 S. chrysomelas 15-16 (3 yr)

11, 26-35

11, 15-34

165, 10-42

28, 16-39

41, 20-45

6, 23-30

5. 37-44

6, 15-43

none

none

1, 26

none

5. 33-40

1, 21

100

100

96

100

100

100

50

0

0

60

0

Pt. Lobos

Big Creek

Hopkins

Pt. Lobos

Big Creek

Hopkins

Hopkins

Pt. Lobos

Big Creek

Hopkins

Pt. Lobos

Big Creek

Pt. Lobos Big Creek

TABLE 4. Total length at which rockfish populations reach 50% sexual maturity (from Wyllie Echeverria 1987) and proportion of fish estimated to be sexually mature from this study.

canopies of all areas (M. Paddack, personal observa-
tion; Lea et al. 1999), rule out this possibility. Larger
sized adults within reserves compared to nonreserves
may cause a relative increase in predation pressure,
although there is no evidence of this. Macpherson et
al. (1997) found no difference in mortality rates of
newly settled fishes between reserve and nonreserve
areas. Nonetheless, the absence of larger predators
might allow juvenile fish outside reserves to reach es-
cape size more quickly, thus causing smaller size class-
es to build up by reducing the time that they are vul-
nerable to predation. Such an effect has been suggested
for sea urchins in a reserve study (Sala 1997).

no data (assume 16)

32-34 (4-6 yr)

27 (4 yr)

37-38 (5 yr)

A final possible explanation for paucity of small fish in reserves is postsettlement migration of recruits due to increased competition or risk of predation. García-Rubies and Zabala (1990) and Goeden (1989, as cited in Roberts and Polunin 1991) had similar results and attributed the lower numbers of small individuals in the reserves to competition for space from the larger (but not more numerous [García-Rubies and Zabala 1990]) individual fish. We observed instances of large fish defending crevice space from smaller conspecifics, a behavior also described by Larson (1980). If there is increased habitat competition within reserves due to a higher proportion of larger fishes defending broader territories, juveniles may respond by moving out of the reserves into adjacent areas. Avoidance behavior has been shown to be driven by the risk of predation in other systems (Huang and Sih 1990, Sala and Zabala 1996).

Biomass/reproductive potential

Different size distributions between reserves and nonreserves also translate into strong effects on bio-

mass, and thus reproductive output. The proportion of sexually mature fish may be greatly reduced by fishing pressure, particularly if the fishery is size selective (Buxton 1993, Sluka et al. 1997). There is evidence of this for deeper water rockfish in California (Ralston 1998). Our data do not indicate a difference in the proportion of sexually mature rockfish between reserves and nonreserves for S. atrovirens, S. chrysomelas, and S. carnatus (Table 4). These three species have similar life histories, each reaching 50% maturity by 15-17 cm (3-4 yr old) (Love et al. 1990, Zaitlin 1986). Alternatively, S. caurinus, S. nebulosus, and S. miniatus grow more slowly (Love et al. 1990) and mature at larger sizes (28-36 cm) (Lea et al. 1999). This, combined with their low numbers may make them more vulnerable to fishing pressure. For these slower-growing species, the proportion of mature fish was greater inside each of the reserves than outside, except for S. miniatus at Big Creek (Table 4). At the nonreserve sites of Hopkins and Pt. Lobos, all of the individuals of these three species encountered were below the length at which they are likely to be sexually mature.

While the proportions of sexually mature individuals overall were not greatly different between reserves and nonreserves in this study, the greater mean size and presence of larger size classes is important. Because of the exponential relationship between length and fecundity, a disproportionate amount of larvae may be produced by the larger size classes, even if they make up a small proportion of the population. In Hopkins Reserve, for example, 55% of the reproductive potential is from fish >31 cm, which make up only 25% of the population.

Larval dispersal

Recent work suggests that the primary benefit of marine reserves to fisheries is through larval dispersal (Buxton 1993, Russ and Alcala 1994, 1996, Rogers-Bennett et al. 1995, Holland and Brazee 1996, Roberts 1997, Allison et al. 1998, Bohnsack 1998, Carr and Raimondi 1998, Morgan and Botsford 1998). Tagging studies have shown limited adult movement and high site fidelity, even for vagile species (Holland et al. 1993, 1996, Miller and Geibel 1973), suggesting that benefits to fished stocks from adult spillover are limited. This may be particularly true on discontinuous reefs (Ault and Johnson 1998).

The major unknown regarding the role of marine reserves is their contribution to the larval pool, and the magnitude of this impact on fished stocks. Modeling studies have shown that increase in the standing stock biomass within marine reserves can enhance or stabilize recruitment to fished stocks (Sladek Nowlis and Roberts 1997, Holland and Brazee 1996). While this prediction has yet to be widely tested, results of some studies provide evidence that larvae from protected populations are sustaining fisheries (Davis and Dodrill 1989, Holland et al. 1996, Stoner and Ray 1996). The high reproductive potential of the reserve areas measured in this study indicate that such an effect is at least possible in central California. Rockfish larvae spend from three to six months in offshore waters (Kendall and Lenarz 1987, Love et al. 1991, Moser and Boehlert 1991), creating the potential for both longdistance dispersal and high recruitment variability due to fluctuations in oceanographic regimes (Love et al. 1998, Ralston and Howard 1995, Ralston and Pearson 1997). Nearshore species have a shortened pelagic phase compared to deeper water species (Moser and Boehlert 1991) which may decrease their dispersal distance (Carr and Reed 1993), creating more localized effects.

Other evidence suggests that most fish replenishment to reefs is from locally retained larvae as opposed to long distance dispersal (Kingsford et al. 1991, Cowen and Castro 1994, Sale and Cowen 1998). Because of this, areas nearby to reserves are likely to be most affected by larval augmentation, and existing marine reserves may be sufficient to augment local stocks but may not significantly enhance fisheries. While the evaluation of reserves for reproductive potential is an important first step, estimates of the fate of the larvae originating from these reserves are imperative for understanding the role these reserves may serve in fisheries management (Carr and Raimondi 1998). Information on mesoscale oceanographic features can be combined with knowledge of location and timing of larval supply in order to infer dispersal routes and distances, and recently developed techniques using otolith microchemistry (Radtke and Shafer 1992) have immense potential for mapping larval movements. Additionally, if dispersal is limited, differences in fish populations should attenuate rapidly with increasing distance from reserves.

CONCLUSIONS

Our findings show a clear difference in kelp forest rockfish populations between marine reserves and unprotected areas in central California. The signal is more evident in the structure of these populations than it is in their abundance. What is less clear is the degree to which these differences reflect the population consequences of human exploitation. There are two main reasons for this uncertainty: the unknown effect of poaching, and the unknown scale of adult and larval movement relative to reserve size. The same uncertainties apply to all or most previously published findings on the effects of marine reserves. Poaching effects are resolvable through monitoring studies or more effective enforcement. The spatial scale question is more difficult to understand, although at least two kinds of information should be useful. One is better data on the spatial ecology of individuals at both the pre and post settlement life stages. Adult (postsettlement) rockfish are presumed to have small home ranges (Larson 1980). However, the degree of exchange between reserves and adjacent exploited areas cannot be inferred from this. For instance, if unexploited rockfish populations are in any way space limited, then a reasonable likelihood exists that reserves and adjacent exploited areas are source-sink systems. Indeed, this is the hope of those who espouse the use of marine reserves for fishery enhancement. The only way to understand these dynamics is by tagging and following the movements and fate of juvenile and adult fish on both sides of reserve boundaries. All open populations are fueled (in a demographic sense) by larval supply (Underwood and Fairweather 1989) and thus understanding the spatial ecology of larvae is also of fundamental importance in assessing the effects and optimal size of marine reserves. The second set of information useful for understanding this issue is comparative data on fish populations at varying distances from marine reserves. Our study contrasted fish populations between reserves and nonreserves that were essentially juxtaposed. Although differences were evident, information on fish population structure at greater distances from the reserves would be highly informative. For example, a continuing reduction in size or density would demonstrate that the true reserve effect was underestimated by our data. Many other important conclusions could be inferred from such information. We urge future studies of marine reserves to focus on these issues.

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