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Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 2010(2010) : 159-179

Published By: American Fisheries Society

URL: https://doi.org/10.1577/C08-056.1

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 2:159–179, 2010

DOI: 10.1577/C08-056.1

[Special Section: Data-Poor Fisheries]

Complementary Sampling Methods to Inform Ecosystem-Based Management of Nearshore Fisheries

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Abstract.—Area-based fishery management and ecosystem-based management strategies are considered beneficial marine resource management tools, but they require finite information about the structure and function of ecosystems to evaluate populations and describe the effects of fishing on ecosystems. The required information is not likely to be obtained from sporadic, fishery-dependent data collected from data-poor fisheries, and funding constraints preclude extensive fishery-independent surveys. This situation has led to an interest in relating or combining information from a variety of disparate sampling methods. From 2003 to 2006, we investigated the relationships between estimates of catch per unit effort (CPUE) and the abundance of fishes generated from typical nearshore commercial fishing operations and estimates of density and abundance derived from scuba surveys in the same locations. The relationships between CPUE and the density estimates derived from different sampling methods were found to be statistically significant in the case of many of the common species sampled across sites in Carmel Bay, California. The compounding effects of within-sample variance and the error associated with the regression equations, however, would result in poor confidence in the values translated from one sampling method to another. Different sampling methods may provide reasonable estimates of population trends, but they are sufficiently different and variable as to preclude the use of a scaling factor to standardize population estimates among sampling methods. Also, the differences in species composition (i.e., relative CPUE or density among species) produced by each sampling method were significant and were also affected by habitat relief and sample depth. Nonetheless, our results suggest the value of a cost-benefit analysis that would allow managers to design optimal sampling strategies for characterizing CPUE relationships within a region of interest. A sampling program that benefits from the complementary strengths of fishing gear and scuba sampling will probably result in the most comprehensive description of nearshore fish assemblages.

In the USA, the Magnuson–Stevens Reauthorization Act of 2006 guides federal fisheries management and mandates the use of annual catch limits and accountability measures to prevent overfishing of federally managed species. This requirement of annual catch limits for federal fisheries has resulted in a large infrastructure to develop fishery management plans, create and evaluate stock assessments, and intensively collect fishery and biological data. To date, these efforts have been focused on high-volume and high-value fisheries in an effort to optimize social and economic benefits from fisheries without overfishing species. However, many marine species are not included in current fishery management plans, and very little information is available with which to evaluate the effects of fishing on nontarget or low-value species. Also, there is growing evidence that it is necessary to manage coastal fisheries on a finer scale to effectively manage nearshore rocky reef ecosystems (Gunderson et al. 2008).

The California Marine Life Management Act of 1998 (MLMA) requires the California Department of Fish and Game (CDFG) to develop management plans for nearshore fisheries that are based on scientific information about stock sizes (Weber and Heneman 2000). During the development of the MLMA, California was experiencing a rapid growth of a live-fish fishery (Leet et al. 2001), and there was a concern that nearshore fish populations were being depleted. The live-fish fishery was expanding rapidly; there was

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Received December 19, 2008; accepted November 10, 2009
Published online April 19, 2010

no effective way to limit effort in the fishery, almost no fishery-dependent information was available, and there was very little fishery-independent data about the life histories of species being harvested. Passage of the MLMA was partly a mandate for CDFG to collect, and use in management, more information about species inhabiting nearshore ecosystems. The MLMA encouraged the use of new ocean management concepts, such as ecosystem-based management (Pikitch et al. 2004). In addition to industry and human-dimension considerations in fisheries management, ecosystem-based management concepts call for increased information about life history characteristics of target and nontarget species as well as more information about the functional relationships among all species in the ecosystem.

Shortly after the MLMA was enacted, CDFG began to collect both fishery-dependent and fishery-independent information on species comprising the nearshore fishery, and developed a Nearshore Fishery Management Plan (CDFG 2006). The Nearshore Fishery Management Plan identified 19 priority species for assessment, the use of essential fish habitat as a management tool, the use of marine protected areas (MPAs) as a fishery management tool, and regional management of nearshore species. It was quickly apparent, however, that the very logical approaches developed in the Nearshore Fishery Management Plan increased the need for information and thus exacerbated problems associated with management of the data-poor nearshore fisheries. The division of California into management regions makes excellent sense from a biological and social standpoint but requires much more information to be collected if the state is going to manage fisheries based on stock assessments. Similarly, the use of marine protected areas as a conservation strategy can create problems with stock assessments, primarily because of two critical reasons: (1) whether or not the fishes in MPAs are counted as part of the stock, and (2) whether or not restrictions on data collection inside MPAs affect the ability to estimate stock sizes (Field et al. 2006). Also, ecosystem-based management strategies will require more information than is currently collected by state and federal agencies. Comprehensive estimates of species abundance, size structure, and the structure of fish assemblages are crucial requirements for assessing both individual fish stocks and assemblage-wide consequences of fishing. This required information is not likely to be available from sporadic, fishery-dependent data obtained from data-poor fisheries and may require comprehensive fishery-independent as well as fishery-dependent surveys.

Most of the fisheries managed by CDFG are considered to be data-poor (Botsford and Kilduff, in press) because there are few stock assessments or catch per unit effort (CPUE) time series indices available for assessing nearshore species in California. Thus, CDFG is considering the possibility of putting together a single index of relative abundance based on using multiple sampling methods (within the same index) because the development of comprehensive (i.e., regional) estimates of stock size may be more cost effective if information is related or combined from a variety of disparate sampling methods, such as a combination of scuba and fishing surveys. The strategy of combining fishery-dependent and fishery-independent information is intriguing but contains several logistical challenges. The primary challenge is to understand the relationships among spatial and temporal variability and the biases associated with each sampling method.

Entire workshops, conferences, and books have focused on the topic of the selectivity and bias of fishing gear (e.g., Gunderson 1993). Much of what has been written relates to the estimation of how representative catches from fishing gear are of the true population structure of target species. In addition to determining if catches provide a biased view of the size, age, or sex structure of a population, fishery scientists often have attempted to quantify the catchability (q) of fishes for use in stock assessments (e.g., Hilborn and Walters 1992). This has led to an understanding of population abundances of some major fisheries (e.g., Worm et al. 2009) that is not available for species in data-poor fisheries. In data-poor fisheries, the emphasis has been on estimating CPUE to form an index of relative abundance to enable fishery scientists to track trends over time (Kruse et al. 2005). In many locations, however, CPUE has been gathered in only sporadic time frames and locations, and from a variety of disparate gear types. The question we are addressing here is the efficacy and reliability of combining disparate estimates of CPUE or density to provide one index of relative abundance that can be used to track population trajectories of nearshore fishes.

As both fishery-dependent and fishery-independent information are collected, it is important to understand what the data represent (i.e., how the different sampling techniques relate to one another, how they are affected by environmental variation, and how they vary in time and space). From 2003–2006, we worked with commercial fishermen, CDFG staff, and university researchers to address five questions. First, are there clear relationships among CPUE–density estimates from different sampling methods, and are these relationships strong enough to use one method as a proxy for another? If not, the lack of a relationship between methods might reflect differences in the influence of habitat and depth on the effectiveness of different sampling methods. Therefore, second, we asked do the relative CPUE (or density) estimates generated by different sampling methods differ according to habitat or depth? Moreover, if two methods generate markedly different estimates of CPUE–density, we asked, third, do surveys conducted by any particular method more accurately or precisely estimate fish abundance compared with estimates generated by mark–recapture techniques? Also, in light of newly developed applications of population size structure for stock assessments of nearshore fishes (O'Farrell and Botsford 2005, 2006), we asked, fourth, how do estimates of size structure differ between these sampling methods? Finally, for assessing effects of fishing on the structure of nearshore fish assemblages, we asked, fifth, do fishing methods differ in their ability to describe the structure of nearshore fish assemblages?

Study Site

To test for potential relationships between CPUE of different survey methods employed by the live-fish fishery (sticks, handlines, and traps) and density from visual scuba surveys, we compared estimates generated by the four methods across four sites sampled in 2003 and two sites sampled in 2005. All the study sites are located in Carmel Bay, Central California (36.53°N, −121.93°W). All sites contained persistent coverage of the giant kelp *Macrocystis pyrifera*, comparable cover of rocky reef substrate, and a depth range of 10–25 m (Figure 1). The area encompassed by each study site ranged from 35,000 to 65,000 m^2.

To further explore whether estimates of species composition, abundance, and CPUE–density generated by different sampling methods varied among reef habitats and depths, analyses were based primarily on the two sites sampled in 2005, which differ markedly in relief and topographic complexity of rocky reef habitat. For these sites, we used multibeam surveys of the sea bottom of Carmel Bay conducted in 2005 by the Seafloor Mapping Laboratory at the CSUMB (http://seafloor.csumb.edu) to identify areas with contrasting rocky reef habitat (Figure 1). The northern site is characterized predominately by low-relief rock habitat, interspersed with coarse sand flats, that contains patches of giant kelp associated with low (<2-m) rock outcrops. The southern site is characterized by continuous high-relief (2–8 m) granitic rock habitat covered with a dense kelp forest. The northern site is surrounded by expanses of sand bottom on all sides, whereas the southern site is surrounded by contiguous high-relief rocky habitat that extends into the Carmel canyon.

Sampling Methods

Fishing estimates of species composition and catch per unit effort

We fished in a standardized manner for 4–6 h/d (from about 0730 hours to 1330 hours) for a total of 12 d at each of the four sites sampled in October and November 2003, and 15 d at each of the two study sites sampled in July, August, and September 2005. The commercial fishermen distributed fishing effort throughout the study site each trip in order to sample each portion of the study site each day. Other than being asked to fish in all parts of the study site, the decisions about where and how to fish were left to the fishermen. Each fisherman used techniques (e.g., bait, soak time, type and number of hooks, traps, or sticks used) commonly used in commercial fishing operations. Fishing methods used included trap, handline, and stick gear. Traps (0.6 × 0.6 × 0.5 m) were deployed singly or on a string of two traps, and usually 10 traps were deployed at a time. Handlines consisted of a weight (approximately 1 kg) and two baited hooks on 40 kg-test fishing line, and were fished for set amounts of time, ranging from 5 to 25 min. Sticks were deployed for approximately 1 h at a time on single lines and buoys, and contained five hooks per stick. Sticks are 1-m lengths of steel bar (1-cm diameter) with five baited hooks on 0.3-m-long leaders attached at uniform intervals along the length of the bar. A line is attached to the bar and buoyed at the surface for deployment and retrieval. We usually deployed 10 sets of sticks at a time. Sticks and traps were typically deployed on the bottom for approximately 1 h. Traps were baited with squid *Loligo opalescens* and anchovies *Engraulis mordax*, whereas sticks and handlines were baited almost exclusively with squid.

All captured species were measured for total length (TL) and released at location of capture. We collected information on species composition, TL, sex (when possible), and the fishing time and depth at which each unit of gear was fished. Actual depth ranges sampled by the different sampling gears across all sample sites were 5–22 m for handlines, 4–26 m for sticks, and 4–22 m for traps. Additionally, at the two sites sampled in 2005, we placed external dart tags in fishes for use in tag–recapture estimates of population sizes. Dart tags were color-coded based on the type of gear used to catch the fish and the location (low-relief or high-relief site) of release. Mortality of tagged fishes was low because we fished in shallow water and handled captured fish carefully. These same techniques resulted in a handling mortality of 1.4–2.4% in a previous study (Starr and Green 2007).

For stick and trap fishing methods, CPUE was

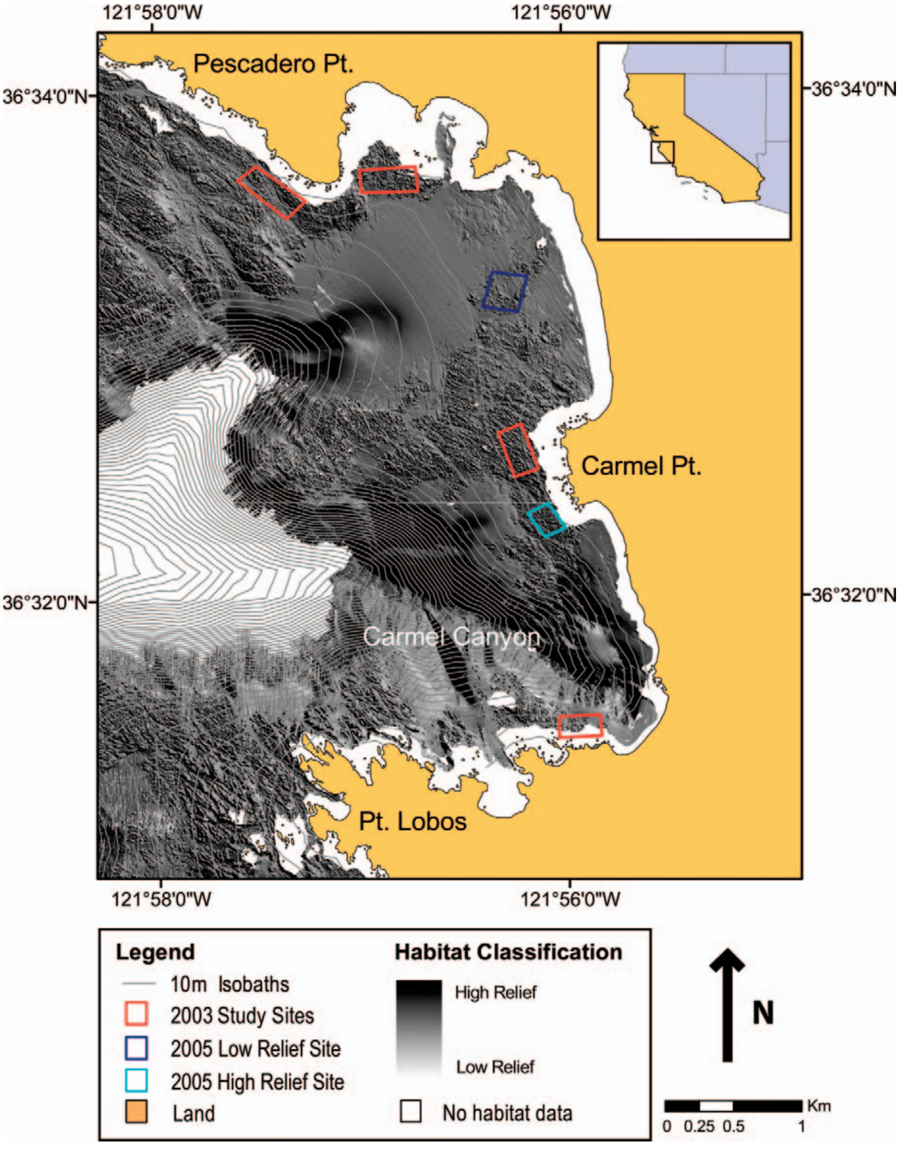

FIGURE 1.—Multibeam images of Carmel Bay, California, depicting the depth contours and topographic relief of study sites sampled in 2003 (red) and 2005 (dark and light blue). This study focuses on the two sites sampled in 2005: the northern, low-relief (dark blue) and southern, high-relief (light blue) sites at the back (east end) of Carmel Bay. Multibeam imagery courtesy of the California State University–Monterey Bay Seafloor Mapping Lab.

calculated by dividing the number of fish caught on an individual stick or trap by the number of hours the method was deployed. Catch per unit effort of hand-lines was calculated by dividing the number of fish caught per angler by the time fished. During the study, if the anglers using handlines did not catch fish within 2–3 min, the skipper relocated the boat and fishing continued in a different spot, frequently one that was only a few meters away. These short (<3-min-long) periods were not recorded, or were included as one longer session.

Scuba surveys of species composition, fish density, and size distributions

Scuba surveys were designed and implemented to meet three specific objectives: (1) provide ground-truthing of the habitat types of the study sites used in 2003 and 2005, (2) estimate the density and size structure of the fish assemblage at each of the study areas using visual strip transects, and (3) generate mark–recapture estimates of abundances of fishes in 2005 based on the resighting of tagged fish by divers.

In 2003, surveys at each study site were repeated on 4 d (between 15 October and 24 November). Each of the two study sites surveyed in 2005 was also sampled on 4 d, 2 d before any fishing occurred (13–16 July 2005) and 2 d after fishing occurred (15–19 August 2005). At each site, four target depth zones were identified, ranging from the deepest at the outer edge of the kelp bed to the shallowest at the inner edge. Actual depth ranges sampled by the divers ranged from 4 to 26 m at sites sampled in 2003 and from 8 to 21 m at sites sampled in 2005. Within each depth zone, six replicate transects were surveyed, roughly parallel to shore and following the depth contours of the reef. Transects were positioned end to end with approximately 10 m of space between replicates. This sampling design produced 96 independent replicate estimates of density for each site. Transects surveyed on the first and second day of these pre- and postfishing survey periods were offset by 20–30 m to avoid resampling the same habitat. Transects consisted of two components surveyed simultaneously by a pair of divers—a benthic and a water column survey. The benthic portion of each transect was 30 m long $\times$ 2 m wide $\times$ 2 m high. The water column component covered an equal volume of water (30 $\times$ 2 $\times$ 2 m) located approximately 5–7 m above the bottom. On each sampling day, two pairs of divers surveyed an entire site, recording the species and estimated TL of all noncryptic fishes (i.e., excluding fishes such as small sculpins and kelpfishes) observed along each transect. In each diver pair, one diver searched for fishes along the bottom, while the other surveyed the water column. Counts from the bottom and water column surveys were pooled for each transect. Density of fishes from scuba surveys was calculated as the mean number of fish seen per transect, which had a 60-m^2 footprint over the substrate. Divers visually estimated TL of every fish observed on all transects to the nearest 1 cm. Divers were trained to estimate fish lengths prior to the study by repeatedly estimating the length of models of known length underwater. Examination of the error in these estimates indicates that divers were typically accurate to within 10% of the TL.

In 2005, after the surface tagging of fishes was finished, divers also recorded the numbers of tagged fishes observed. In addition to counting tagged fishes on the visual strip transects, divers conducted roving diver surveys on four other days to estimate tagged-to-untagged ratios of fishes. On those days (22, 23 August; 28 September; and 5 October), pairs of divers divided each study area into shallow and deep halves, and counted tagged and untagged fishes as they swam from one end of a study site to the other so as to avoid recounting individuals they previously encountered. Divers used dive lights to identify and record the color of each tag. Because the tagging effort included midwater species, divers surveyed the bottom and middle of the water column separately for tagged fishes.

Analysis methods: are there relationships among catch-per-unit-effort–density estimates from different sampling methods, and are these relationships strong enough to use one method as a proxy for another?

We performed a robust regression analysis using an MM estimation (Yohai et al. 1991) to examine the strength of regression relationships among CPUE estimates from different fishing methods and the potential for using one method to predict the expected values of another method. Mean CPUE estimates were calculated for each of the sites surveyed by divers and fishermen in both 2003 and 2005. Fishing and scuba samples taken on multiple days at a site were pooled, and the resulting site mean values from the two survey years were combined in the same analysis. These values were tested for normality using the Shapiro–Wilk test and square root transformed to meet assumptions of normal distributions and homoscedasticity. In a regression analysis of this type, which compares estimates of CPUE of one sampling type with another, large measurement errors can be associated with both the dependent and independent variables. As a result, ordinary least-squares regression can be overly sensitive to outliers, particularly in the explanatory variables (leverage points). Robust estimation using the MM estimation method provides estimates of model parameters, which are robust (i.e., not sensitive to small departures from model assumptions) and resistant to outliers in both the explanatory and response variables (SAS, version 9.1.3).

When significant slope values were detected using robust regression, the utility of these relationships (e.g., sticks versus scuba) was further evaluated by calculating confidence intervals (CIs) on estimates of the response variable predicted at various levels of the explanatory variable. Error associated with these predicted values scales with the product of sampling error associated with estimates of the explanatory variable, and statistical error associated with the slope of the regression equation. The upper and lower confidence limits of the CPUE–density estimates were multiplied by the upper and lower confidence limits of the slope to generate a CI on the predicted level of the response variable. Using these extrapolated CIs, it was possible to determine whether a given difference in the explanatory variable would result in a statistically detectable difference in the response variable.

Do differences in catch per unit effort–density from the different sampling methods vary with habitat or depth?

To determine whether relative CPUE–density differed among sampling methods and if any differences varied with habitat and depth, data from the two sites (of low- and high-rock relief) sampled in 2005 were used to test for interactions between sampling method and site, sampling method and depth, and sampling method, site, and depth. A univariate analysis of variance (ANOVA; SAS, version 9.1.3) was used for each of the nine most abundantly sampled species: cabezon *Scorpaenichthys marmoratus*, kelp greenling *Hexagrammos decagrammus*, lingcod *Ophiodon elongatus*, black rockfish *Sebastes melanops*, black-and-yellow rockfish *S. chrysomelas*, blue rockfish *S. mystinus*, gopher rockfish *S. carnatus*, kelp rockfish *S. atrovirens*, and olive rockfish *S. serranoides*. Divers were unable to differentiate olive rockfish from yellowtail rockfish *S. flavidus* underwater, so those species were treated as a group in the analyses. In the analysis for each of these species, sampling method and site (low versus high relief) were both treated as fixed variables. Third-order and then second-order interaction terms involving the continuous covariate (depth) were sequentially removed from the model when they were nonsignificant, resulting in a reduced model for each species, mean squared error being correctly attributed to the remaining error terms. Prior to analysis, any differences in scale of CPUE–density between habitats were removed from the data by standardizing observations within each habitat across sampling methods (mean = 0; SD = 1).

Do surveys conducted by any particular sampling method more accurately or precisely estimate fish abundance compared with estimates generated by mark–recapture techniques?

We used two methods to estimate population sizes of fishes in each of the 2005 study site areas. First, we multiplied mean density estimates (fish/60-m^2 transect) from scuba visual transects by the area of each study site to obtain population estimates. This extrapolation approach, which involves taking the mean of multiple transects surveyed on multiple days, provided estimates of abundance that summarize variability occurring across both spatial and temporal scales, and enabled us to generate 95% CIs around mean estimates for all species observed in the scuba surveys. Second, we used the multiple-sample Schnabel mark–recapture method to estimate population size of the more-abundant species inhabiting each study site (Krebs 1989). Total number of tagged individuals of each species was pooled across the different fishing methods. Total number of recaptures was pooled across fishing methods and tagged fishes sighted by divers. The Schnabel method assumes that the population is closed (i.e., minimal emigration), all animals have the same probability of capture (i.e., samples are random), tagging does not affect catchability, and tags are not lost. We assumed that we met the assumptions of the Schnabel method because the majority of the study species have high site fidelity and small home ranges relative to the study areas (Freiwald 2009), the duration of the study was short (reducing the likelihood of emigration from the study area), and the tagging and recaptures pooled across sampling methods reduced sampling bias of any single sampling method (i.e., individuals were sampled randomly). Combining the high proportion (54%) of resightings by divers with recaptures by fishing minimizes the potential effect of tagging on the probability of recapture (i.e., catchability). The Schnabel method has an advantage over alternative mark–recapture (e.g., Peterson) methods in that it enabled us to treat information from multiple days, allowing us to increase the sample size of population estimates. This increased sample size resulted in greater precision of population estimates. However, for the scuba surveys, we had insufficient samples for all fish species resighted to be analyzed using the Schnabel method. Therefore, we invoked the Petersen method for three groups of tagged fishes (kelp rockfish, olive rockfish–yellowtail rockfish complex, and kelp greenling) sighted by divers. All assumptions were the same for both the Schnabel and Petersen methods.

Relative accuracy of the fishing method CPUE estimates and the density estimates from scuba surveys in relation to "total" abundance estimates from the mark–recapture method were evaluated using linear regression. Estimates from each method for the nine commonly sampled species at both the low- and high-relief sites sampled in 2005 were used as replicates. Because abundance estimates extrapolated from scuba data provide a means of scaling the density estimates to correspond to populations within the boundaries of each study site, we again tested for correlation against mark–recapture abundance estimates, in this case testing for a one-to-one relationship (i.e., slope equal to one).

Precision estimates (i.e., ratio of variation to the mean) were also compared among sampling methods and mark–recapture estimates. Confidence intervals (95%) standardized to the mean were used to compare the precision of abundance estimates between the mark–recapture and extrapolation of scuba density estimates.

How do estimates of size structure differ among sampling methods?

Using the data collected from the low- and high-relief sites sampled in 2005, we compared length frequency distributions for the nine commonly sampled species in the study. Two-sample Kolmogorov–Smirnov (K–S) tests were used to compare length frequency distributions for all pairwise combinations of sampling methods, pooling observations from the low- and high-relief sites. Length frequency comparisons were run in three different ways: (1) using all observations from each method regardless of fish length; (2) using only fishes with estimated TLs of 20 cm or greater to account for the fact that fishing methods caught very few individuals below this limit, while scuba divers often saw them in high numbers; and (3) using only length observations of tagged individuals to reduce the possibility of a size-selective sampling bias between methods (i.e., observations came from a known subset of the population).

In these multiple K–S tests, we did not correct (reduce) the critical *P*-values to avoid type II error (detecting a difference in size distributions when, in fact, there is none) in order to maximize our ability to detect any sampling bias between sampling methods. Here, the consequence of type II error (falsely concluding that there is sampling bias) is considered less egregious than committing type I error (concluding that different sampling methods sample size distributions similarly when, in fact, they do not), leading to the inappropriate comparison of size distributions generated from different sampling methods and possible misinterpretation of sample bias as spatial and temporal differences in size distributions. Moreover, when comparing the relative magnitude of bias among sampling methods, the "significance" (critical *P*-value) is less important than the relative *P*-values and, for this reason, we present these relative *P*-values of the multiple tests. Similarly, pairwise tests were run comparing the low- and high-relief sites with regard to the sensitivity of each sampling method in detecting differences in length frequency distributions between locations.

Do sampling methods differ in their ability to describe assemblage structure?

The four sampling methods were evaluated on their ability to describe nearshore fish assemblages in terms of species richness. In order to determine the relative number of samples required of each sampling method to characterize the entire fish assemblage, species accumulation curves were generated using a resampling procedure to estimate the mean number of species recorded with increasing levels of sampling effort for each method (i.e., numbers of sticks, traps, handlines, or scuba transects; Primer, version 6). Because the relationship between sampling effort and the number of species observed indicates how well an assemblage would be represented given increased or decreased levels of sampling effort, we evaluated how many samples from each method would be required to obtain a greater than 95% probability of seeing at least one individual of a given species. Additionally, we calculated how many of the nine most commonly caught species would be detected in 50 samples of each method.

To determine whether characterization of fish assemblage structure differed among different sampling methods (scuba surveys, traps, sticks, and handlines), we tested for differences in the species composition (i.e., relative CPUE–density) of fishes larger than 20-cm TL of the nine species that were sampled in common by the four sampling methods. Since habitat and depth were suspected to interact with the effectiveness of different sampling methods (see question 2 above), these terms were also included in the analysis. As a result of the limitation on degrees of freedom imposed by testing these effects across a large number of species, multivariate ANOVA could not be employed and a nonparametric method—permutational multivariate ANOVA (PERMANOVA)—was used (Anderson 2001; McArdle and Anderson 2001). In this approach, mean CPUE–density estimates were calculated for each day of sampling for each of the sampling methods at each site. Each of these community samples was standardized (equal total across species) to remove scale differences between sampling methods. A similarity matrix was then calculated, and pairwise distance values between groups of samples were used in an algorithm analogous to the parametric ANOVA approach.

Results

We fished for a total of 25 boat fishing-days and caught a total of 2,684 fish from 17 different species (Table 1). The total number of fish caught at each site was similar; we caught 1,239 fish at the low-relief site and 1,445 fish at the high-relief site. The TL of more than 99% of the fish caught was 20 cm or longer. Divers counted a total of 4,756 fish from 29 species (1,229 fish from 24 species at the low-relief site and 3,527 fish from 27 species at the high-relief site). The total number of fish greater than 20 cm long observed on quantitative transects (2,088), however, was less than the number of fish caught by fishing methods.

TABLE 1.—Percentages of individuals of each species observed (scuba) or caught (sticks, handlines and traps) for all study sites combined.

Species	Scuba	Sticks	Handline	Traps
Blue rockfish *Sebastes mystinus*	62.2	21.5	54.5	1.9
Striped seaperch *Embiotoca lateralis*	8.0			
Painted greenling *Oxylebius pictus*	4.9			
Gopher rockfish *Sebastes carnatus*	4.3	45.0	16.4	51.3
Black rockfish *Sebastes melanops*	4.1	5.0	13.2	0.9
Kelp rockfish *Sebastes atrovirens*	3.9	2.8	2.3	2.8
Olive/yellowtail rockfish *Sebastes serranoides/flavidus*	2.6	0.7	1.7	
Kelp greenling *Hexagrammos decagrammus*	1.9	0.4	0.2	1.3
Black-and-yellow rockfish *Sebastes chrysomelas*	1.7	14.2	8.8	35.0
Pile perch *Rhacochilus vacca*	1.2			
Señorita *Oxyjulis californica*	1.2			
Lingcod *Ophiodon elongatus*	0.6	3.5	1.8	0.3
Blackeye goby *Rhinogobiops nicholsii*	0.6			
Black perch *Embiotoca jacksoni*	0.6			
Rainbow seaperch *Hypsurus caryi*	0.4			
Tubesnout *Aulorhynchus flavidus*	0.3			
Vermilion rockfish *Sebastes miniatus*	0.3	2.4	0.2	
Cabezon *Scorpaenichthys marmoratus*	0.2	1.1		3.1
Rubberlip seaperch *Rhacochilus toxotes*	0.2			
Kelp perch *Brachyistius frenatus*	0.1			
China rockfish *Sebastes nebulosus*	0.1	0.6	0.2	0.6
Copper rockfish *Sebastes caurinus*	0.1	1.7	0.9	0.6
California sheepshead *Semicossyphus pulcher*	0.1			
Wolf-eel *Anarrhichthys ocellatus*	<0.1	0.1		
Speckled sanddab *Citharichthys stigmaeus*	<0.1			
Rock greenling *Hexagrammos lagocephalus*	<0.1			1.9
Sixspot prickleback *Kasatkia seigeli*	<0.1			
Thornback *Platyrhinoidis triseriata*	<0.1			
Treefish *Sebastes serriceps*	<0.1	0.6		
Spiny dogfish *Squalus acanthias*		0.6		
Grass rockfish *Sebastes rastrelliger*				0.3
Total number of fish	4,756	1,041	1,323	320
Total number of species	29	15	11	12

Are There Relationships among Catch-per-Unit-Effort–Density Estimates from Different Sampling Methods, and Are These Relationships Strong Enough to Use One Method as a Proxy for Another?

Robust regression analysis demonstrated significant positive relationships between CPUE–density estimates for seven of the nine species sampled in common by different sampling methods (Table 2). Only CPUE–density for kelp rockfish and lingcod showed no correlation among any of the sampling methods compared. Relationships between CPUE–density estimates for stick versus handline and scuba versus stick were the strongest, there being significant slope values for five and three out of nine species, respectively. When all species were combined into a single overall CPUE–density estimate, only the regression between

TABLE 2.—Summary of the results of robust regression analysis of the relationships between CPUE estimates from different sampling methods across the six sites surveyed in either 2003 or 2005 for the nine most frequently caught fishes. Significant relationshipss ($P < 0.05$) are denoted by bold italics.

Species	Scuba versus handline	Scuba versus stick	Scuba versus traps	Traps versus handline	Traps versus stick	Stick versus handline
All fish species	0.8164	0.7917	0.1385	0.1619	0.3685	***0.0019***
Kelp rockfish	0.8883	0.6927	0.4811	0.9005	0.5431	0.7435
Gopher rockfish	0.2919	***0.0249***	0.2977	0.5259	0.0814	0.8888
Black-and-yellow rockfish	0.1634	***0.0153***	0.3365	0.7744	0.3583	0.1614
Black rockfish	0.4145	0.7678	0.995	0.4391	0.586	***0.011***
Blue rockfish	0.8719	0.4902	0.7268	***0.001***	***0.0386***	***<0.0001***
Olive/yellowtail rockfish	0.5452	0.8413				***0.0055***
Kelp greenling	0.5305	0.9965	0.2194		0.0457	
Lingcod	0.8757	0.252	0.3634		0.0589	0.3678
Cabezon	***0.0031***	***0.0328***	0.5931	0.2792	0.4355	***0.039***

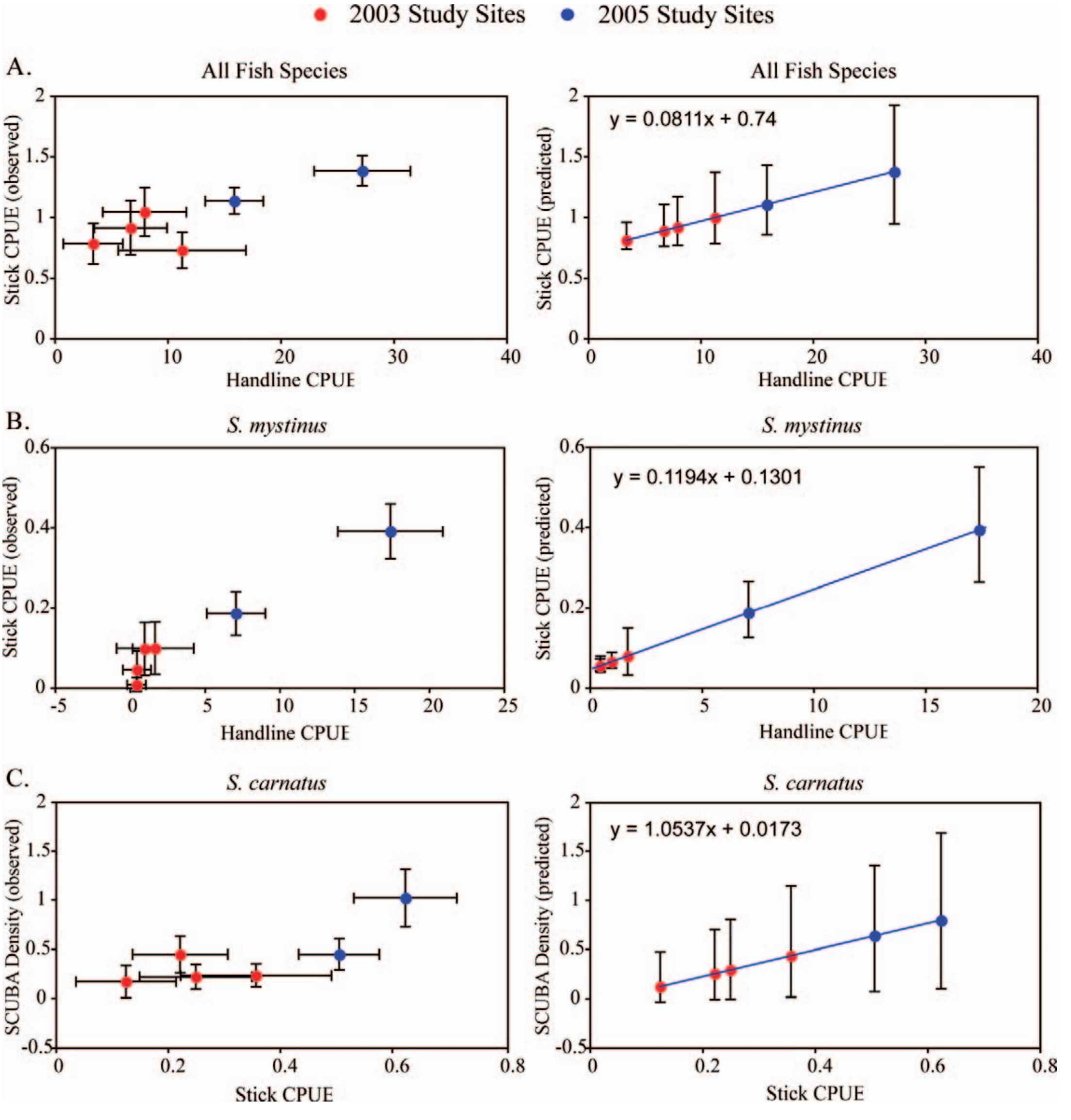

FIGURE 2.—Correlations between CPUE estimates from different sampling methods: **(A)** handlines versus sticks for all species (i.e., total number) of fish caught, **(B)** handlines versus sticks for blue rockfish, and **(C)** sticks versus scuba for gopher rockfish. The graphs on the left show the mean CPUE estimates for each site, the error bars representing the 95% confidence intervals around the means. The points in red represent the four sites sampled in 2003, those in blue the low- and high-relief sites sampled in 2005. In the graphs on the right, the values on the *x*-axis are the same mean CPUE estimates, while those on the *y*-axis are the values predicted by the robust regression equation.

sticks and handline methods showed a significant relationship. Significant relationships for scuba versus trap were not detected in any species, and only one species (cabezon) showed a significant relationship for scuba versus handline.

Confidence intervals were calculated around predicted CPUE–density values for each of the significant regression equations (Figure 2, graphs on the right). The width of these CIs as a percentage of the predicted value ranged from an average of 12.7% for blue rockfish to an average of 70.0% for cabezon. There was a high degree of overlap in these CIs across the range of observed CPUE–density values for all but one of the species with significant sampling method regressions, such that an observed increase in the value of the predictor variable would not result in the

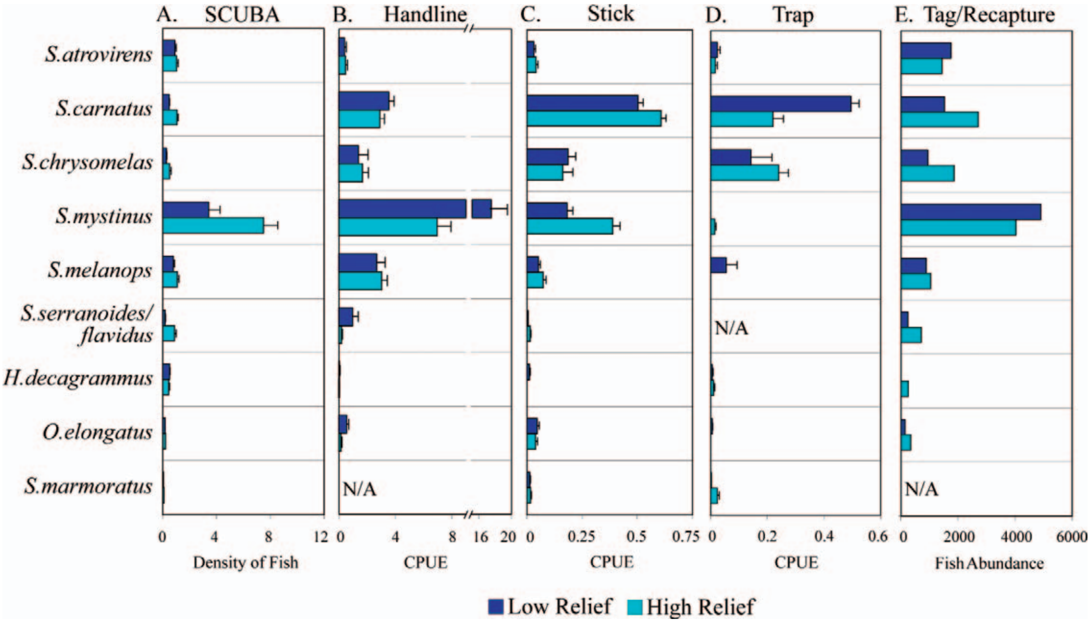

FIGURE 3.—Estimated species composition of the nine most abundant species (see Table 2) sampled in the northern, low-relief (dark blue) and southern, high-relief (light blue) sites by **(A)** scuba (fish per transect) and **(B)** handlines, **(C)** sticks, and **(D)** traps (all measured in CPUE or catch/h). Abundance estimates (**E**) were obtained using tag–recapture from all observations of tagged and untagged fish (from scuba, sticks, traps, and handlines).

expectation of a significant difference (increase) in the response variable. This was the case whether all species were combined or examined individually (e.g., gopher rockfish; Figure 2C). The one exception to this was blue rockfish, where the relationship between handline and stick CPUE estimates had narrower CIs (Figure 2B). However, using points on the graph as an example, it would require almost a 10-fold increase in handline CPUE from 1.7 to 17.0 to result in a discernibly higher predicted value of stick CPUE.

Do Differences in Catch per Unit Effort–Density from the Different Sampling Methods Vary with Habitat or Depth?

There were strong differences in estimates of CPUE–density of each of the nine common species among the different sampling methods as indicated by highly significant *P*-values for most species (Figure 3; Table 3). Generally, scuba and handline had greater CPUE than sticks or traps for many species (note the differences in scale of the horizontal axes of Figure 3). Significant three-way interactions between the main effects in the ANOVA model (sampling method, site [i.e., habitat relief and depth]) were detected in four species (kelp rockfish, gopher rockfish, black-and-yellow rockfish, and blue rockfish), suggesting that differences in CPUE among methods are influenced by both depth and relief. As expected, density of gopher rockfish increased and density of black-and-yellow rockfish decreased with increasing depth (Table 3); however, this effect differed among sampling methods, and interpretation of two-way interactions (method × depth, site × depth, or site × method) for these species is not possible given the significant three-way interaction. Two groups (lingcod and the olive rockfish–yellowtail rockfish complex) did show significant two-way interactions between sampling method and depth; in both cases, handline CPUE decreased with depth while scuba density increased with depth. Lingcod also exhibited a significant site × method interaction, suggesting that for this species, relief may influence the effectiveness of sampling methods differentially. The remaining three species (black rockfish, kelp greenling, and cabezon) showed no significant interactions between sampling method and either site or depth.

Do Surveys Conducted by any Particular Method More Accurately or Precisely Estimate Fish Abundance Compared with Estimates Generated by Mark–Recapture?

Fish tagged during the first round of sampling at the two sites surveyed in 2005 were recaptured by fishing methods and observed by divers during a second round of sampling conducted a month later. Of the total

TABLE 3.—*P*-values from ANOVA tests of the effects of sampling method, site (= habitat relief), depth, and their interactive effects on the CPUE of nine kelp forest fishes. *P*-values in bold italics denote significant (< 0.05) relationships. Terms removed from the final reduced model for each species are indicated as n.s.

Species	Method	Site	Depth	Method × site	Method × depth	Site × depth	Method × site × depth
Kelp rockfish	***0.0019***	***<0.0001***	0.1468	***<0.0001***	0.8174	***<0.0001***	***<0.0001***
Gopher rockfish	***0.0010***	0.1014	***<0.0001***	0.0824	***<0.0001***	0.0755	***0.0273***
Black-and-yellow rockfish	***<0.0001***	0.2283	***<0.0001***	***0.0110***	***<0.0001***	0.1072	***0.0213***
Black rockfish	***<0.0001***	0.6296	0.8940	0.1242	n.s.	n.s.	n.s.
Blue rockfish	***<0.0001***	***<0.0001***	0.1324	***<0.0001***	0.3309	***<0.0001***	***<0.0001***
Olive/yellowtail rockfish	***<0.0001***	0. 1135	0.6636	0.1262	***0.0011***	n.s.	n.s.
Kelp greenling	***<0.0001***	0.9305	0.9035	0.8677	n.s.	n.s.	n.s.
Lingcod	***<0.0001***	***0.0194***	0.2434	***<0.0001***	***0.0013***	n.s.	n.s.
Cabezon	***<0.0001***	0.7591	0.0540	0.6927	n.s.	n.s.	n.s.

number of fishes tagged (1,697), a combined total of 342 were subsequently "recaptured" by one of the sampling methods. The majority of these second observations (54%) were visual observations of tagged fishes by scuba divers either on transect or during random swims through the sample areas. The stick sampling method resulted in the highest rate of fishing recaptures of tagged fishes (13%, or 92 of 687 individuals), followed by handline (8%) and traps (2%). Among species, gopher rockfish had the highest rate of recapture of tagged fishes (15%). Recapture rates were lower for black rockfish (3%) and were lowest among kelp greenling, kelp rockfish, and olive rockfish–yellowtail rockfish (<2%). The number of fishes observed, tagged, and recaptured was similar between the two sites.

We compared CPUE–density estimates from each sampling method for the most commonly sampled species with mark–recapture abundance estimates generated using both fishing and scuba observations (Figure 4). Scuba density estimates had the highest correlation with mark–recapture abundance (Figure 4A; $r = 0.811$, $P = 0.0002$), followed by handline CPUE ($r = 0.809$; $P = 0.0003$) and stick CPUE ($r = 0.684$; $P = 0.0049$). Trap CPUE was not significantly correlated with abundance ($r = 0.240$; $P = 0.3894$). Abundance estimates derived by extrapolating scuba densities to the total area of each study site had a higher degree of correlation with mark–recapture abundances than the original density estimates (Figure 4B), and the slope of this relationship was not significantly different from 1 ($P = 0.654$), indicating a one-to-one correspondence between the two.

We calculated mark–recapture population estimates using recaptures from fishing gear only and also using both fishing recaptures and diver resightings combined (Figure 4C). There was generally close agreement between these two approaches both in terms of the relative abundance of different species and the relative population size of each species at the low-relief site versus the high-relief site.

Based on our sample sizes, precision of CPUE–density estimates was low for all species and sampling methods as indicated by coefficients of variation (CV = 100 × SD/mean) ranging from 100% to 1,700% (Figure 5). Precision was similar among sites and gear for the abundant gopher rockfish and black-and-yellow rockfish, but differed markedly among sampling methods for other species. For all species except blue rockfish, estimates of CPUE–density from scuba had the lowest CV (i.e., highest precision), followed by handlines, sticks, and traps. Precision was lower in the low-relief site than in the high-relief site for the majority of species and across sampling methods, corresponding to the patchy distribution of fishes seen in the discontinuous habitat at the low-relief site.

Lastly, we evaluated the relative precision of the population estimates derived from both extrapolation of scuba densities and from mark–recapture using all sampling methods, in this case by plotting the 95% CIs expressed as a percentage of the mean (CI/mean; Figure 6). Smaller CI–mean ratios reflect higher precision. The precision of abundance estimates generated by the extrapolation of scuba density was generally higher than those from the tag–recapture method. Surprisingly, these precision estimates from extrapolation of scuba density and tag–recapture estimates show an opposite pattern between the low-relief site and the high-relief site: CI–mean ratios of the former tended to be higher at the low-relief site, whereas those of the latter were higher at the high-relief site in all but one case.

How Do Estimates of Size Structure Differ among Sampling Methods?

Comparisons of length frequency distributions generated by the different sampling methods based on all individuals (i.e., all lengths) showed that the

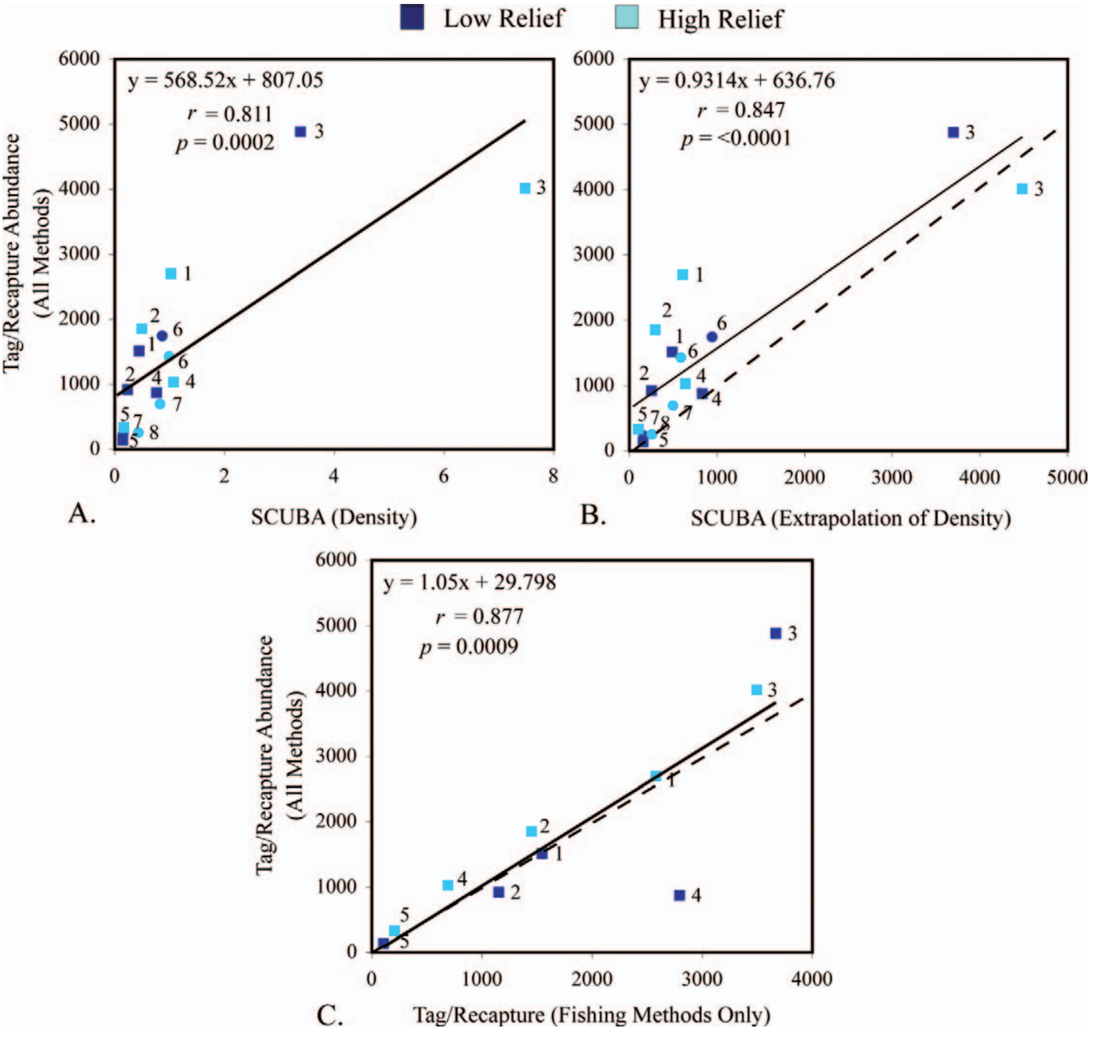

FIGURE 4.—Correlations between density and abundance estimates for commonly sampled species in the northern, low-relief site (dark blue) and southern, high-relief site (light blue): **(A)** density from scuba surveys versus mark–recapture abundance estimates based on fishing and scuba surveys, **(B)** abundance extrapolated from scuba density versus mark–recapture abundance based on fishing and scuba, and **(C)** mark–recapture abundance based on fishing methods only versus mark–recapture abundance based on fishing and scuba. For (C), only five fish species had enough samples to be used in the analysis for fishing methods only. Mark–recapture data represented by squares denote all data analyzed with the Schnabel method; data represented by circles were analyzed by the Petersen method. The dotted lines in (B) and (C) are the identity lines, at which the abundance estimates would indicate direct correspondence between methods. The species used in these analyses are as follows: (1) gopher rockfish, (2) black-and-yellow rockfish, (3) blue rockfish, (4) black rockfish, (5) lingcod, (6) kelp rockfish, (7) olive/yellowtail rockfish, and (8) kelp greenling.

strongest differences in lengths (smallest *P*-values) occurred between scuba and the other sampling methods, especially for the more abundant species (Table 4). These differences reflect the greater number of smaller individuals that is sampled by scuba compared with the other methods. Few differences in length distributions were detected among the fishing methods (sticks, traps, handline) or the less-abundant species. A similar pattern of differences persists when individuals greater than 20-cm TL were compared (Table 4), indicating that the presence of smaller individuals in the length frequency data from scuba surveys was not solely responsible creating dissimilar distributions. However, when length frequency distributions based only on tagged individuals greater than 20-cm TL were compared among sampling methods,

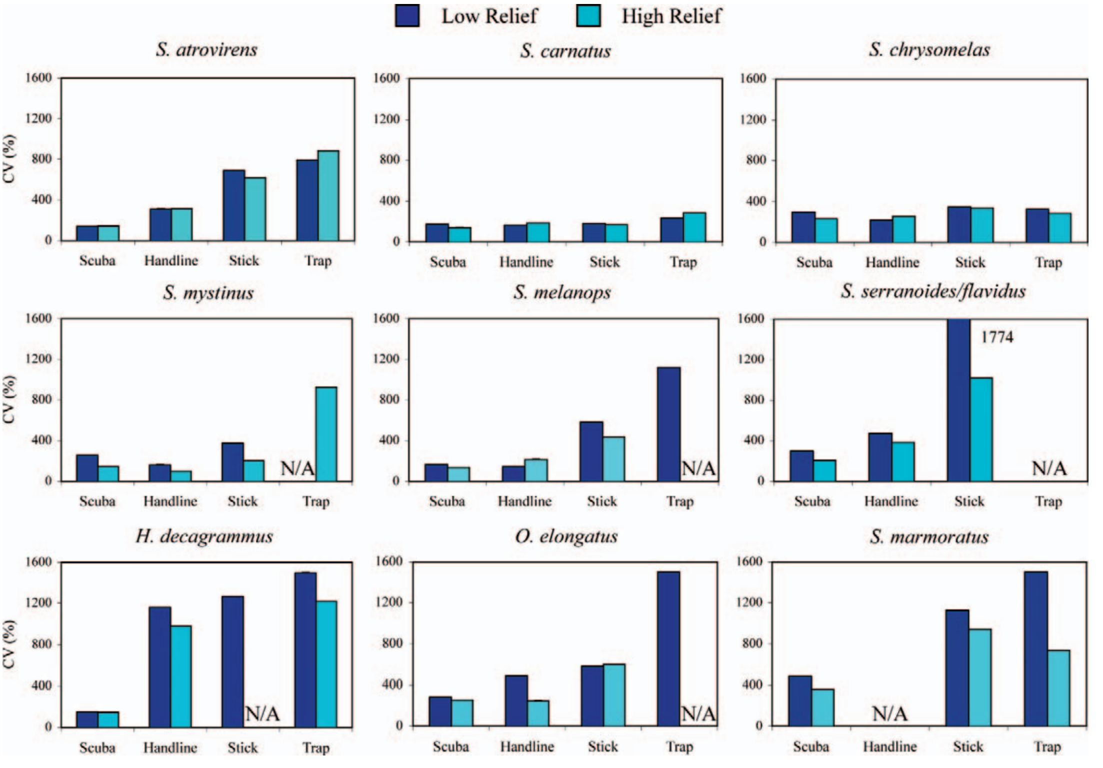

FIGURE 5.—Relative precision of the CPUE–density estimates generated by the different sampling methods. Plotted are the coefficients of variation (CVs; expressed as percentages) of the nine most abundant species sampled in the northern, low-relief (dark blue) and southern, high-relief (light blue) sites by scuba, handline, stick, and trap methods.

differences were less pronounced (larger P-values) for all paired comparisons. Despite these differences in frequency distributions, estimates of mean length of individuals greater than 20-cm TL were very similar among all sampling methods and species in both low- and high-relief habitats (Figure 7).

Comparison of length frequency distributions between the two study sites showed that all the sampling methods tended to show equal sensitivity in detecting potential differences between populations (Table 5). Across the four sampling methods, significant differences in length distributions among the low- and high-relief sites were detected in five of the nine commonly sampled species. Of these five species, only one, kelp rockfish, showed any disagreement between sampling methods. Significant differences were detected by scuba and sticks, which sampled this species in relatively high numbers, but not by traps or handline, where it was recorded less frequently.

Do Sampling Methods Differ in Their Ability to Describe the Structure of Fish Assemblages?

Overall, estimates of the species composition of the sampled fish assemblage (i.e., relative CPUE–density of the nine most abundantly sampled species) differed among the different sampling methods (Table 1; Figure 3). Sticks, traps, and handline methods caught about the same number of species, but the number of individuals of each species caught varied among the sampling methods. Scuba surveys recorded two to three times the number of species and four to fifteen times the number of individuals that were recorded by the fishing methods (Table 1).

Of the 15 species caught with fishing methods, scuba sampled the most species and handline gear sampled the fewest (15 and 11 species, respectively; Table 6; Figure 8). Traps required far more samples than any other sampling method to sample a representative number of species caught (9) and recorded far fewer species for a representative number of samples (50) than any of the other methods, reflecting the selectivity of the sampling method. It also required far more samples to detect 95% of all the species caught (Figure 8). Of the sampling methods examined, scuba recorded, on average, the highest number of species (12) for a given number of samples (50) and required the fewest number of samples (11) to detect a representative number of species, reflecting the higher

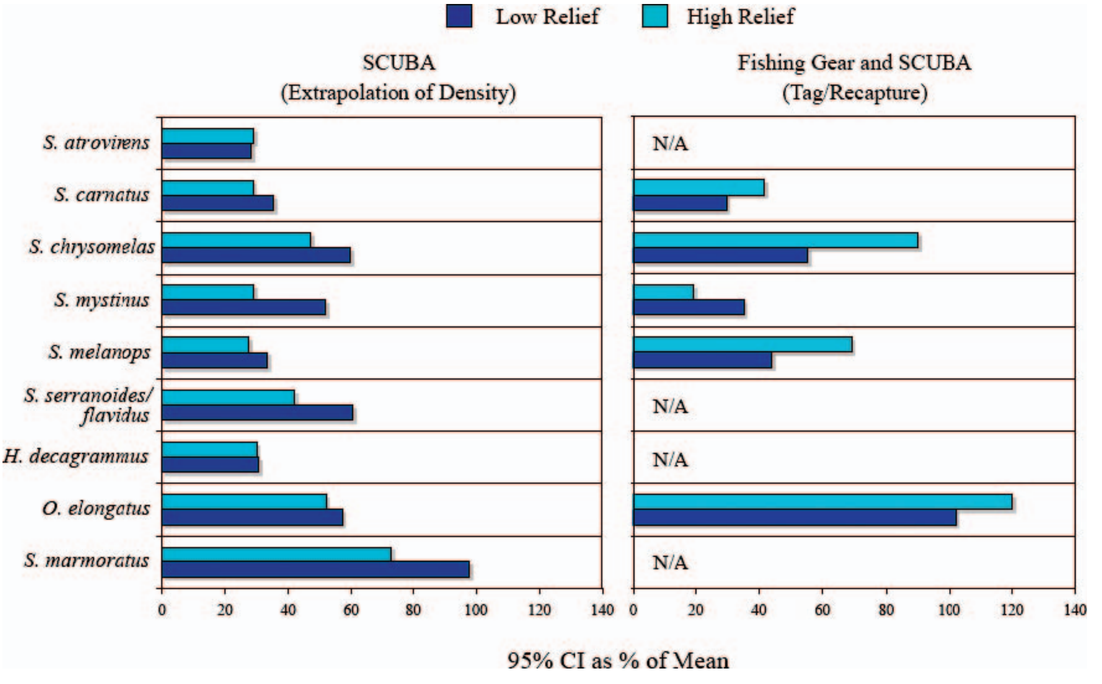

FIGURE 6.—Relative precision of the population estimates generated by the extrapolation of scuba density estimates and tag–recapture methods. Plotted are the 95% confidence intervals (CIs) expressed as percentages of the means for the nine most common species for the northern, low-relief (dark blue) and southern, high-relief (light blue) study sites; N/A = not applicable.

number of species encountered on a transect sample compared with a stick, trap, or handline. Surprisingly, scuba surveys were remarkably efficient at detecting cryptic species, such as lingcod and cabezon. The number of samples required to obtain a greater than 95% probability of seeing at least one individual lingcod ranged from 26 for scuba (60-m^2 transects) to 29 for handlines, 95 for sticks, and 503 for traps (hours fishing). The number of samples required to obtain a greater than 95% probability of seeing at least one individual cabezon ranged from 44 samples for scuba to 161 samples for traps. Cabezon were not caught on handlines.

Differences in patterns of species composition among sampling methods (i.e., relative CPUE–density of the nine commonly sampled species) varied according to depth (PERMANOVA sampling method $\times$ depth interaction term: df = 3, $P = 0.002$). Species composition also differed significantly between the low- and high-relief sites (df = 1; $P = 0.005$); however, these site differences did not vary according to sampling method (method $\times$ site interaction: df = 3, $P = 0.435$) and the three-way interaction (method $\times$ site $\times$ depth) was also not significant (df = 3; $P = 0.764$).

Discussion

Are There Relationships among Catch-per-Unit-Effort–Density Estimates from Different Sampling Methods, and Are These Relationships Strong Enough to Use One Method as a Proxy for Another?

Relationships among CPUE–density estimates from different sampling methods were found to be statistically significant in the case of many of the common species sampled across sites in Carmel Bay in 2003 and 2005. Generally, regression equations between handline and stick or scuba and stick sampling methods demonstrated the closest fit. The strongest regression (i.e., narrowest CI on the estimate of the slope) occurred in the most-abundant species (blue rockfish), weaker relationships occurring in less-abundant or less-common species such as gopher rockfish and cabezon.

Similar relationships between research fishing CPUE and visual census data have previously been reported in the literature (Richards and Schnute 1986; Haggarty and King 2006); however, the potential for using these regression equations as an aid to stock assessment and management decisions, as yet, has not been fully evaluated. As an example, resource managers may at some point need to incorporate CPUE data from fishing to fill in spatial or temporal gaps in visual census data in order to generate regional stock assessments or to

TABLE 4.—*P*-values for comparisons of size frequency distributions between sampling methods using paired-sample Kolmogorov–Smirnov tests for the nine common species based on all individuals recorded, only individuals >20 cm TL, and only tagged individuals >20 cm TL. Length frequencies from the low- and high-relief sites are combined. Empty cells indicate that there were insufficient data for the tests.

Species	Stick versus traps	Stick versus handline	Trap versus handline	Stick versus Scuba	Trap versus Scuba	Handline versus Scuba
All fish (all sizes)						
Kelp rockfish	0.1096	0.5639	0.0881	<0.0001	0.0037	<0.0001
Gopher rockfish	0.9196	0.2395	0.2134	<0.0001	0.0000	<0.0001
Black-and-yellow rockfish	0.5413	0.7471	0.9510	<0.0001	<0.0001	<0.0001
Black rockfish	0.2773	0.1240	0.6935	<0.0001	0.9942	<0.0001
Blue rockfish	0.0419	<0.0001	0.0036	<0.0001	0.0001	<0.0001
Olive/yellowtail rockfish		0.0143		0.0012		0.1601
Kelp greenling	0.2106	0.8928	0.1389	0.2824	0.2579	0.7263
Lingcod	0.3557	0.3201	0.5176	0.0249	0.7454	0.3242
Cabezon	0.2293			0.8877	0.8372	
All fish (>20 cm TL)						
Kelp rockfish	0.1096	0.5639	0.0881	<0.0001	0.0060	<0.0001
Gopher rockfish	0.8033	0.3060	0.1758	<0.0001	0.0001	<0.0001
Black-and-yellow rockfish	0.5413	0.7738	0.9966	<0.0001	<0.0001	0.0001
Black rockfish	0.2773	0.1240	0.6935	<0.0001	0.9766	<0.0001
Blue rockfish	0.0430	<0.0001	0.0037	<0.0001	0.0016	<0.0001
Olive/yellowtail rockfish		0.0188		0.0076		0.9399
Kelp greenling	0.2106	0.8928	0.1389	0.3001	0.2741	0.7085
Lingcod	0.3557	0.3201	0.5176	0.0249	0.7454	0.3242
Cabezon	0.2293			0.8877	0.8372	
Tagged fish only (>20 cm TL)						
Kelp rockfish	0.4727	0.9153	0.6787	0.1231	0.9900	0.2372
Gopher rockfish	0.5613	0.1328	0.0357	0.0002	0.0006	<0.0001
Black-and-yellow rockfish	0.1313	0.4118	0.9316	0.4041	0.0660	0.1636
Black rockfish	0.2541	0.0487	0.6821	0.0011	0.7365	0.0136
Blue rockfish	0.3372	<0.0001	0.0595	<0.0001	0.0727	<0.0001
Olive/yellowtail rockfish		0.0227		0.0478		0.8728
Kelp greenling	0.5176	0.9963	0.2700		0.9963	0.5176
Lingcod	0.3585	0.2999	0.5758	0.0137	0.3752	0.0062
Cabezon	0.1745					

evaluate MPA effectiveness. In this study, we found that the compounding effects of within-sample variance and the error associated with regression equations would result in poor confidence in values translated from one sampling method to another. Even in the case of blue rockfish, which had the narrowest CIs on predicted values, a 100% difference in stick CPUE values between locations could not be used to predict a significant corresponding difference in handline CPUE.

The significant relationships we observed are notable because the data contained a high degree of variability associated with pooling data from different sites, seasons, and years. The predictive capacity of these relationships may be improved by increasing sampling effort in two possible ways. Increasing the number of replicate subsamples (scuba transects, sticks, traps, or handlines) at each site would reduce CIs of the mean values used as predictor variables in the regression relationship. Increasing number of sites (i.e., spatial or temporal replicates) used to characterize the relationship would both increase accuracy and reduce CIs of model parameters and thus allow increased confidence in predicted values of response variables.

Differences in relative CPUE estimates among species obtained from the sampling gear used in this study suggest possible selectivity biases for one or more types of gear (i.e., catching proportionally more or less of a particular species than would be predicted by its actual abundance). However, regression relationships comparing the density estimates for individual species between sampling methods will not be affected by this selectivity bias unless competition for hooks–traps occurs. In this event, CPUE estimates for a particular sampling gear and species may go up or down depending on the local abundance of other species with positively biased catch rates for that sampling gear. It may be possible to model the effects of this type of selectivity bias using mark–recapture data that represent "true" abundance estimates to calibrate the selectivity of various sampling methods for important species. This information, when combined with catch–effort relationships, may allow us to assess whether, at a given level of sampling effort, gear

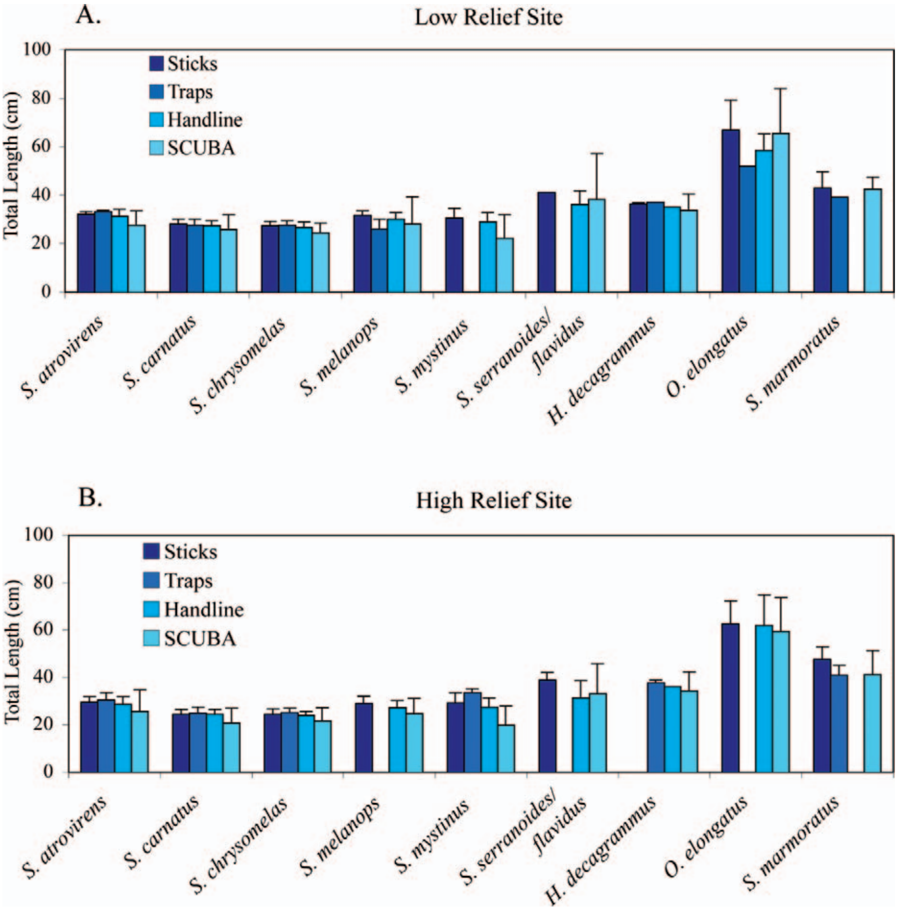

FIGURE 7.—Mean TL (cm) and SDs for the nine most abundant species in **(A)** the northern, low-relief site and **(B)** the southern, high-relief site. The size-frequency data were truncated to include only fish with TLs of 20 cm or longer.

availability is likely to influence catch rates for less-selected species. Whereas increasing sample size will not eliminate these biases, it is possible that higher levels of replication will result in both (1) increased confidence in population estimates and regression relationships among methods, and (2) saturation of sampling effort such that CPUE of less-selected species will not be influenced by density of more-selected species.

The results of this study also suggest the possibility of a cost-benefit analysis that could allow managers to design optimal sampling strategies for characterizing CPUE–density relationships within a region of interest. The analysis would combine a comparison of the effort required to either sample at more sites or sample fewer sites more intensively with a resampling simulation that would provide an estimate of the corresponding reductions in CIs of either the model parameters or the predictor variables. The result would be an estimate of

TABLE 5.—Differences in length distributions between high- and low-relief sites for each sampling method, as determined by two-sample Kolmogorov–Smirnov tests for fish ≥20 cm. Single asterisks denote a significant difference in length frequency distributions ($P \leq 0.05$), double asterisks denote a highly significant ($P \leq 0.001$) difference, "ns" equals no significant difference, and blanks indicate insufficient data for the tests.

Species	Sticks	Traps	Handline	Scuba
Kelp rockfish	*	ns	ns	**
Gopher rockfish	**	**	**	**
Black-and-yellow rockfish	**	**	**	*
Black rockfish	*		**	*
Blue rockfish	*		**	**
Olive/yellowtail rockfish				ns
Kelp greenling				ns
Lingcod	ns		ns	ns
Cabezon	ns	ns		ns

TABLE 6.—Comparison of species accumulation curves among the different sampling methods (Figure 8). Plot values were calculated using simulated groupings of increasing numbers of samples.

Variable	Scuba (all species seen)	Scuba (fished species)	Sticks	Traps	Handlines
Total number of species sampled	29	15	15	12	11
Number of species expected to be encountered in 50 samples	23	12	8	5	9
Number of samples required to encounter 95% of total species sampled	147	158	351	411	131

the levels of model sensitivity (i.e., whether a given "effect size" could reliably be translated from one type of data to another) that would result from increased or reallocated sampling effort.

Do the Relative Catch-per-Unit-Effort–Density Estimates Differ According to Habitat or Depth?

Estimates of CPUE–density generated by the different sampling methods were significantly influenced by habitat and depth as evidenced by significant interactions between these terms and sampling methods for many of the species sampled in this study. This result is to be expected given the selectivity of fishing methods for different species and what is known about the specificity of depth ranges and habitat preference of nearshore fishery species (Miller and Lea 1972; Eschmeyer and Herald 1983; Love et al. 2002; Allen et al. 2006). The implications of these interactions are that (1) a single calibration or correction cannot be applied to correct CPUE in the regression model of one sampling method with another if sampling with different methods differs by depth or relief; (2) rather, the depth and relief effects would have to be accounted (i.e., controlled) for by restricting sampling to comparable depths and relief across the geographic range in which the relationship will be applied; or (3) depth- and relief-specific corrections would have to be generated.

Do Surveys Conducted by Any Particular Method More Accurately or Precisely Estimate Fish Abundance Compared with Estimates Generated by Mark–Recapture Techniques?

Significant correlations occurred between mark–recapture abundance estimates and CPUE–density estimates from scuba, sticks, and handlines. Of the various sampling methods, density estimates from scuba showed the highest correlation to mark–recapture estimates, and this pattern was strengthened more when comparing abundance estimates derived from scuba densities by extrapolating them to the area of each study site. This improvement of the correlation by applying a differential scaling factor between the two sites indicates that the area in which tagged and untagged individuals are moving is larger in the low-relief than in the high-relief site and, therefore, that the densities in the low-relief site must be multiplied by a larger number to correctly correlate them to mark–recapture abundance estimates. Although great effort was made to fish uniformly within the same defined area used by divers for scuba transects, it is possible that areas of sand between reef habitat patches, particularly at the northern, low-relief site, would result in differences in the area of available habitat between sites. This suggests that habitat mapping techniques (e.g., multibeam sonar) could be used to improve the correspondence of density or CPUE estimates to mark–recapture abundance estimates and improve translation between these types of data.

The precision of both CPUE–density and abundance estimates from this study was low as evidenced by the poor predictive ability of regression relationships between methods. However, there was greater precision in estimates of some methods (i.e., scuba and handline) than others (i.e., sticks and traps). There was also greater precision in estimates from the contiguous habitat of the high-relief site than from the patchy

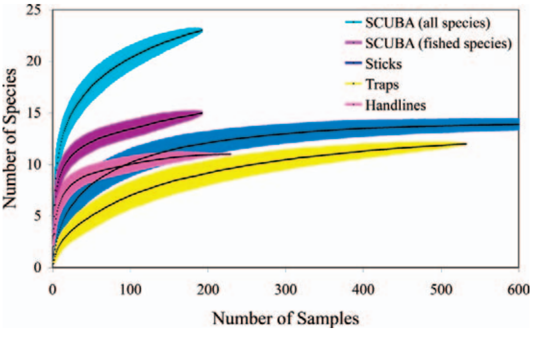

FIGURE 8.—Species accumulation curves for scuba (using a data set containing all species seen by divers), scuba (using a data set limited to species observed by all fishing methods), sticks, traps, and handlines. The plotted values are the mean numbers of species seen in simulated groupings of increasing numbers of samples. The colored areas show the SDs above and below the mean values.

habitat of the low-relief sites. This suggests again that efforts to integrate relative abundance or CPUE–density estimates among different sampling methods will require information on habitats sampled and further studies using higher replication in suitable and carefully matched habitats to better calibrate relationships between methods.

Tagged fish were resighted at a greater rate using scuba than they were recaptured by any of the fishing methods. This had the result of increasing the sample size of tagged to untagged fish ratios and improving confidence in the resulting abundance estimates generated by the Schnabel method. This presents a considerable complementary benefit of using both diving and fishing to assess relationships between density and abundance: more individuals can be tagged in an area using fishing, and for many species, the proportion of those individuals to the larger population can be better assessed using scuba.

Our interpretations of the relative accuracy of the different sampling methods assume that the abundance estimates generated by the Schnabel tag–recapture method are accurate. We believe we met the key assumptions of this method for the reasons mentioned in the Methods section. However, if populations in the study area were not closed (especially with substantial emigration from the study area) or experienced substantial tag loss, or if tagged fish reduced their likelihood of recapture (catchability), our estimates would likely overestimate the true abundance. If rates of tagging and recaptures were biased by one or more sampling methods such that individuals were not randomly sampled (e.g., only a portion of the size distribution or a particular habitat was sampled), we would have likely underestimated the true abundance of a species and misrepresented the relative abundance of species. Although we designed the study to minimize these sources of error, actual tests of these assumptions will greatly inform this and other assessments of sampling methodology.

How Do Estimates of Size Structure Differ among Sampling Methods?

There was generally good correspondence of mean lengths estimated by each of the fishing methods for fishes larger than 20 cm, and differences in mean length and size frequency between the two sites were detected similarly for most species by all four sample methods. However, size-frequency distributions estimated by scuba for most species were often significantly different from those estimated by the fishing methods. When we used all of the diver data, including fish smaller than 20 cm, it was apparent that length frequencies derived from diver observations spanned a greater range (both larger and smaller fish), and divers often saw more fish at the lower end of the frequency distributions. This bias may be explained in two possible ways: either the visual estimation used by scuba divers introduces greater measurement error into size estimates, or divers are accurately observing a larger population of sizes for most species than that selected by each type of fishing method. When size frequencies are compared using only tagged individuals, which represent a subsample of the actual population with known lengths, size frequencies were more comparable and significant differences were seen less frequently. This suggests the latter of the two possibilities above, that diver observation is less selective than fishing gear with respect to size, and size frequencies estimated by visual census more accurately reflect the natural population.

This has important implications if size- or age-structured models will be used to estimate population status of nearshore species (O'Farrell and Botsford 2005, 2006). On one hand, it confirms the accuracy of length measurements made by divers using visual estimation, and on the other, it suggests a potential hazard of comparing data from different fishing methods due to the size selectivity imposed by different gear types.

Do Sampling Methods Differ in Their Ability to Describe the Structure of Fish Assemblages?

Although fishing surveys can obtain more information about biological parameters of fishes such as weights and ages, scuba divers can visually quantify greater numbers of fish at any given point in time than can be caught and recorded using any of the fishing sampling methods used in this study. In addition, the rates at which the bottom (area) or water column (volume) are sampled are much greater using scuba transects than with any of the fishing methods. Aside from resulting in higher counts of most species, this difference means that the rate at which individual species are encountered is higher on scuba transects (i.e., higher slope of the species accumulation curve; Figure 8) such that fewer samples and less time are required to obtain an estimate of the structure of the fish assemblage in nearshore rocky reef or kelp habitats. For example, the resampling analysis of transect, stick, handline and trap data shows that to encounter the nine most-abundant commercial species, the scuba method would require, on average, 11 transects and 2 h of work for a two-diver team, as opposed to 7, 16, and 18 h of work with sticks, handlines, and traps, respectively.

The total number of species observed using scuba (29) was much higher than was observed using sticks

(15), traps (12) or handlines (11), indicating that visual observations are less selective than fishing methods and provide more complete data on presence or absence of individual species and overall community structure. Many of the species that were only observed using scuba were not fished species but are nevertheless important in terms of characterizing the composition of nearshore assemblages, particularly if management goals (e.g., evaluating MPA effects) involve ecosystem-based management. The only fish to be recorded using a fishing method, but not observed by divers, was the spiny dogfish, a highly mobile species seen relatively infrequently in kelp forests.

A common conception among both fisheries scientists and fishers is that certain species that are rare, cryptic, or commonly concealed within the structure of the reef will be undersampled by scuba surveys relative to fishing methods. Surprisingly, lingcod and cabezon were encountered more frequently using scuba than with fishing gear. Resampling simulations showed that for both of these species, far fewer samples would be required to acquire a 95% probability of encounter on a scuba transect than when using any fishing method. One of the reasons for the low encounter rate of some species, however, is that certain fishes occupy relatively specific habitat types. Some species, such cabezon and the brown rockfish *S. auriculatus*, for example, more commonly inhabit low relief areas that are not abundant in Carmel Bay. Fishing gear is more efficient at sampling some species (e.g., grass rockfish and wolf eel *Anarrhichthys ocellatus*). All of the species that were caught with fishing gear are commercially important, but some recreationally important species (e.g., sea perches Embiotocidae and California sheephead) were not recorded using fishing gear at the levels of sampling effort employed in this study. For this reason, a sampling program that benefits from the complementary strengths of both fishing gear and scuba sampling will likely result in the most comprehensive description of nearshore assemblages. The combination of fishing to tag and recapture fishes along with scuba tag–recapture surveys may provide an especially good estimate of population abundances of nearshore fishes.

Summary

Area-based fishery management and ecosystem-based fisheries management strategies are being presented as a means of moving towards ecosystem-based management and to improve marine resource use and conservation. These new resource management tools require more finite information about the structure and function of ecosystems in order to be effective. One way to gather the additional spatial and temporal information needed is to combine data from a variety of fishery-dependent and fishery-independent sampling methods. As fishery-dependent and fishery-independent information are collected, however, it is critical to understand the relationships between the types of data (i.e., how estimates generated by the different sampling techniques compare with one another and how they are affected by environmental variation).

In this study comparing several types of fishing and scuba sampling methods in kelp habitats on temperate rocky reefs, there was generally good correspondence among all fishing methods for estimates of mean lengths for that portion of the population greater than 20 cm long. Size-frequency distributions estimated by scuba were significantly different from those estimated by each fishing method for most species, primarily because divers counted smaller fish than were caught with fishing gear. Relationships among CPUE–density estimates from different sampling methods were found to be statistically significant in the case of many of the common species sampled. However, CPUE–density estimates were significantly influenced by habitat and depth. The variety of sampling methods provided similar estimates of differences between the low-relief and high-relief study sites. A comparison of abundance estimates generated by mark–recapture techniques indicated that the extrapolation of scuba densities had greater precision than did other sampling methods.

Given the similarities among CPUE–density estimates from different sampling methods, it might be possible to use a variety of sampling tools to determine large differences in fish communities along the coast. The compounding effects of within-sample variance and the error associated with regression equations, however, would result in poor confidence in values translated from one sampling method to another. Thus, different sampling methods may each provide reasonable estimates of population trends but are sufficiently different and variable so as to preclude the use of a scaling factor to standardize population estimates among sampling methods.

Our analyses indicate that accuracy and correspondence among a variety of sampling methods can be increased by increasing the number of sites used to characterize nearshore fishes. By adding spatial or temporal replicates, it would be possible to both increase accuracy and reduce CIs of model parameters and, therefore, increase the predictive value of response variables. Additional studies are needed to determine what levels of increased sampling are required to provide a scaling factor suitable for adequately standardizing population estimates. Despite the uncertainties in developing comparable population estimates from different sampling tools, given that each sampling method has its strengths and limitations with respect to species, depths, habitats sampled, and logistical ease of sampling, we believe that trends in populations of nearshore communities are best characterized by using a combination of fishing gear and scuba sampling methods. The differences among the sampling methods, however, strongly indicate that different sampling methods should not be used as proxies for one another.

Acknowledgments

This project was funded by the Partnership for Interdisciplinary Studies of Coastal Oceans, California Sea Grant Program, Commonweal Foundation Ocean Policy Program, Pacific States Marine Fishery Commission, and the University of California Division of Agriculture and Natural Resources. We would like to acknowledge the CDFG (especially Dave Osorio) for logistical and field support. We thank the following for assistance with field data collection and for fishing surveys: D. Ardizzone, K. Blackhart, D. Benet, M. Burford, K. Cox, C. Dawson, J. Duryea, J. Felton, J. Figurski, J. Freiwald, K. Green, J. Grover, B. Hughes, A. Jensen, S. Lonhart, S. Lucas, D. Moreno, D. Osorio, R. Skrovan, P. Serpa, P. Tompkins, and especially T. Wadsworth. Special thanks to commercial fishermen Sal Pitruzzello and Giovanni Nevoloso, whose knowledge of fishing and collaborative efforts were invaluable to this project. The analysis in this manuscript benefited greatly from many thoughtful discussions and advice from P. Raimondi and the comments of two anonymous reviewers. This work was conducted under a permit from and with the support of National Oceanic and Atmospheric Administration's Monterey Bay National Marine Sanctuary. This is contribution number 329 from the Partnership for Interdisciplinary Studies of Coastal Oceans, funded primarily by the Gordon and Betty Moore Foundation and David and Lucile Packard Foundation.

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