Title

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MARINE RESERVE DESIGN: OPTIMAL SIZE, HABITATS, SPECIES AFFINITIES, DIVERSITY, AND OCEAN MICROCLIMATE

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Abstract. The design of marine reserves is complex and fraught with uncertainty. However, protection of critical habitat is of paramount importance for reserve design. We present a case study as an example of a reserve design based on fine-scale habitats, the affinities of exploited species to these habitats, adult mobility, and the physical forcing affecting the dynamics of the habitats. These factors and their interaction are integrated in an algorithm that determines the optimal size and location of a marine reserve for a set of 20 exploited species within five different habitats inside a large kelp forest in southern California. The result is a reserve that encompasses ~42% of the kelp forest. Our approach differs fundamentally from many other marine reserve siting methods in which goals of area, diversity, or biomass are targeted a priori. Rather, our method was developed to determine how large a reserve must be within a specific area to protect a self-sustaining assemblage of exploited species. The algorithm is applicable across different ecosystems, spatial scales, and for any number of species. The result is a reserve in which habitat value is optimized for a predetermined set of exploited species against the area left open to exploitation. The importance of fine-scale habitat definitions for the exploited species off La Jolla is exemplified by the spatial pattern of habitats and the stability of these habitats within the kelp forest, both of which appear to be determined by ocean microclimate.

Key words: biological-physical coupling; conservation; habitat; kelp forest; Macrocystis; *marine protected area; marine reserve; reserve design; reserve size; stability.*

INTRODUCTION

The most important objective of coastal zone management is to ensure long-term ecosystem services, especially with regard to conserving biodiversity and sustainable human use of the system. A fundamental management objective is the protection of ecosystem processes that maintain species and their natural relationships. Zonal management recognizes the mutually exclusive nature of some of these ecosystem services with exploitation and attempts to optimize between protective and extractive needs.

While design criteria of "no-take" marine protected areas (referred to here as reserves) are much discussed, most established reserves have serendipitous origins and result from managers taking advantage of politically feasible opportunities. Unfortunately, many such reserves are chosen to avoid political conflict and represent suboptimal habitats. The attractive idea of networked reserves begs the obvious problem of a network based on a system of non self-sustaining reserves that are doomed to collapse with or without the network. Thus it

is important to understand the parameters of a self-sustaining system so that eventual networking can be built on robust components. Eventually, society needs a network of reserves as hedges against catastrophe (Sala et al. 2002, Allison et al. 2003) as well as for building a system that might also contribute to renewal of exploited stocks (Murray et al. 1999, Hastings and Botsford 2003).

A robust network of reserves is difficult to design because it depends both upon the individual reserves being self-sustaining as well as an objective understanding of their connectivity (Halpern and Warner 2003, Roberts et al. 2003). Presently neither are understood for marine systems, and connectivity processes, while much discussed, are not well understood even for the commercially important species, much less for other species. Here we focus on defining a self-sustaining "no-take" reserve in a well-known habitat. Our explicit objectives were to identify and protect critical habitats of exploited species, and to evaluate the physical forcing factors that determine the important spatial and temporal patterns.

With regard to the open-ended question about optimal reserve size, we recognize that the answer depends upon specific questions and case-by-case ecosystem components that need protection. To be
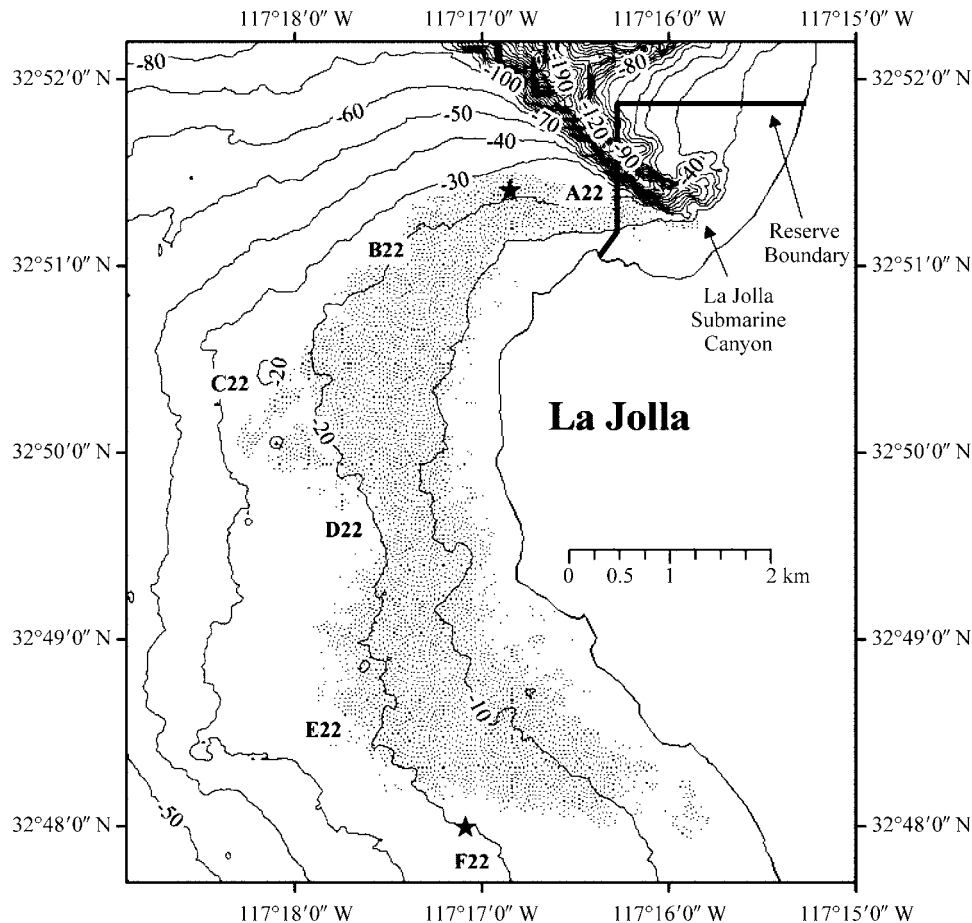
FIG. 1. Map of the La Jolla kelp forest (stippled area where *Macrocystis pyrifera* has been observed at least once in aerial photographs taken 1967–1999) and submarine canyon. The boundary of the San Diego–La Jolla Ecological Reserve (area, ~2.16 km²) is shown as a thick line. Bottom temperature was recorded at stations A22–F22 along the 22-m contour. Positions of two bottom-mounted ADCPs (acoustic doppler current profilers) are indicated by stars. Bathymetric units are meters. Note that the position of A22 appears to be inside the kelp bed but was actually >150 m outside during the study.

successful, reserves need to be large enough to include and sustain the important populations that spend most of their time within the immediate area. This includes a reasonable definition of habitat essential to all local life-history components of the core species (but see Halpern et al. 2005 for discussion of other components). Recognizing that it is not possible to include all aspects of essential habitat for all species, we attempt an evaluation of essential habitat to define the reserve size that optimizes the trade-off between protection and exploitation needs. It is not possible to be more specific and still general.

The goal of our project was to develop a method for optimizing the design of marine reserves in shallow water, coastal habitats. The study was conducted in the La Jolla kelp forest, the second largest kelp forest off California (Fig. 1). Results of extensive ecological habitat surveys were used in a Monte Carlo simulation to determine an optimal size and location for a reserve within the kelp forest. Historical data on the stability of

the kelp forest and physical oceanographic data were used to explore the potential mechanisms that give rise to persistent ecological variability across the study area. While this study was conducted within the context of a specific site, the methods developed should be broadly applicable to designing marine reserves in other temperate or tropical habitats. The design recognizes that inherent tradeoffs often exist between the value and the cost of marine reserves, both of which tend to scale with the size of a reserve. For example, a large reserve will generally afford protection to a greater number of species (Halpern 2003) and habitat types than a small reserve and can thus be said to have a higher ecological value. However, the political, societal, or financial costs of creating and enforcing large reserves may be far greater than for small ones. Similarly, reserves that are too small to adequately protect species or habitat types of interest may have acceptable costs but little ecological value. Developing tools to assess the ecological value of

a reserve and to examine how value scales with size is therefore a critical step in designing marine reserves.

The La Jolla kelp forest offers a gradient of habitats and includes part of a small (~2.16 km²) "no-take" reserve that also protects a rare submerged canyon-habitat system as well as shallow rocky-reefs and a sloping sandy shelf (Parnell et al. 2005). Here we propose an optimal reserve designed to protect twenty exploited species that inhabit the La Jolla kelp forest using a quantitative approach based on the physical, biological and oceanographic components of the system that are collectively most critical for them. By necessity, the design of a reserve in La Jolla must be based on site-specific information including habitats as well as the biological and physical factors that might affect the resilience and stability of these habitats. This is true of any study where optimal reserve design is a goal. Here we present a case study, in which biological and physical data were collected and analyzed with the goal of determining habitat distributions and importance, and the resilience and stability of the system.

METHODS

Research strategy

The overall approach in this study can be summarized as three phases. Phase I consisted of discriminating and mapping subhabitats within the kelp forest and estimating the affinity of each exploited species to these subhabitats (cf. species-specific habitat utility). In phase II, we determined an optimal size and location for a reserve to collectively protect the set of 20 exploited species using a simple and generally applicable algorithm. The reserve was designed based on the spatial patterns of subhabitats, their species-specific importance, and adult (exploited life phase) mobility. Phase III consisted of using historical data on the spatial stability of the kelp forest and new physical data to explore the mechanisms driving habitat structure and stability within the kelp forest to help understand the spatio-temporal dynamics of the forest and therefore gauge the stability of the reserve over time.

The steps within phase I were as follows: (1) we estimated the underlying scale of habitat variability (i.e., the spatial scale necessary to encompass a range of habitat features such as reefs and sumps) to determine an appropriate scale over which to stratify our biological and habitat surveys; (2) we conducted surveys of habitat parameters and the abundance of 61 species of fish and invertebrates at random locations throughout the kelp forest, stratified by the spatial scale estimated in step one (250 m); (3) these results were used to define and locate subhabitats within the kelp bed and to estimate species affinities for those subhabitat types; and (4) species affinities to the subhabitat types were used to assign a relative habitat utility of each subhabitat for each species.

In phase II, we used estimates of species mobility obtained from the literature along with the information obtained from phase I to determine an optimal size for a reserve in the kelp forest for the set of 20 exploited species using a Monte Carlo approach. This was accomplished by the development and application of an algorithm to estimate the relative value of important habitats for all exploited species off La Jolla based on our survey data of habitats and species, the spatial distribution of these habitats, and the adult mobilities of these species. Practical constraints associated with the need for simple boundaries were then imposed to determine the ideal location for our optimally sized reserve.

In phase III, we (1) analyzed historical data on the location of the La Jolla kelp canopy over the past ~50 yr; (2) collected and analyzed temperature and current data at locations across the study area for potential spatial differences in temperature that may reflect differential nutrient availability, and differences in currents, indicative of variable fluxes of nutrients and larvae through the system; (3) analyzed modeled wave energy to determine the spatial distribution of wave climate throughout the kelp forest; and (4) collected and analyzed demographic data on sea urchins, an important kelp grazer to assess potential differences in recruitment for this species across the forest given the differences in ocean microclimate that we observed (see *Results*). Spatial differences in urchin recruitment are known to affect spatial patterns of kelp community dynamics thereby affecting habitat quality, resilience, and stability.

Study site

The nearshore habitat off La Jolla (Fig. 1) is dominated by hard bottom substrata interspersed with small patches of sand and cobble. At its fullest extent, the kelp forest off La Jolla is over 8 km long and is up to ~1.5 km wide. The forest narrows to ~600 m near the middle and is bordered by sand on the northern, southern, and offshore margins. The nearest kelp forests are ~7 km distant from the northern and southern edges of the La Jolla forest. The Del Mar kelp forest, to the north, is small (~1.2 × 0.4 km) and ephemeral, while the Pt. Loma kelp forest is the largest kelp forest in California (~10 × 1.25 km). The extreme northern margin (~0.7%) of the La Jolla kelp forest is protected within the San Diego–La Jolla Ecological Reserve, established in 1971. The La Jolla area is remote from municipal wastewater discharge and does not receive waters from industrialized or agricultural watersheds, estuaries, or bays. There have been no documented effects of pollutants on the marine ecosystem off La Jolla.

Biological component

Kelp forest habitats.—Kelp forest surveys were conducted during late spring and summer of 2002 using stratified random band transects (30 × 4 m) within the entire area that kelp canopy has been observed at least

once from aerial surveys between 1967 and 2002. A pilot study was conducted to determine the spatial scales of habitat variability (distance between reefs and sizes of habitat patches such as pavement, rock fields, and sand patches) within the kelp bed to develop an optimal spatial scale for stratification. This suggested a stratification grid of ~250 m spacing. Random locations within each grid box were then surveyed. Habitat parameters included depth and sharp vertical relief which were determined every meter along the line, type of substrate (bedrock, rock, cobble, sand), and algae every 0.5 m, and the presence/absence of important habitat-forming bottom features (reefs, ledges, crevices, overhangs) within 5-m sections. Sixty-one species of conspicuous animals were surveyed in the band transects, 20 of these species have been fished recreationally and/or commercially within the Southern California Bight.

Major habitat types were determined using hierarchical divisive clustering analysis (Kaufman and Rousseeuw 1990) of substrate, bottom features, vertical relief, and algal data (see Parnell et al. 2005 for details). Utilization of the resulting habitats by exploited species (habitat breadth; Ludwig and Reynolds 1988) was calculated as a measure of habitat specificity for these species. For the present case, habitat breadth indicates the average number of habitats utilized by each species. The most important combination of habitat characteristics that correlated to the set of exploited species (20 species) was determined using the BIO-ENV procedure (Clark and Ainsworth 1993).

Survey data were also used to determine the spatial distribution of species diversity throughout the forest. Diversity was estimated for each transect (Hill's $N1$ diversity $e^{H'}$, Hill 1973, where H' is Shannon's index) using data from all 61 species. These values were then spatially interpolated to a raster map using ordinary kriging in ArcView (ESRI, Redlands, California, USA).

Sea urchin size frequencies.—The red sea urchin, *Strongylocentrotus franciscanus*, is presently the target of the most valuable fishery in kelp forest habitat off California and the dynamics of this species are of special interest for reserve design. Red sea urchins and the nonexploited purple sea urchin, *S. purpuratus*, are important herbivores in southern California, capable of exerting strong grazing pressure on kelps (North et al. 1991) and therefore affecting the quality of habitat for other species. Equally important, the spine canopy of red sea urchins provides an important nursery habitat for juvenile sea urchins and abalone (Tegner and Dayton 1977). We estimated spatial patterns of size structure for both urchin species by revisiting sites where they were found to be abundant in random band transects. Urchins were collected exhaustively from haphazardly placed 1-m^2 quadrats and brought to the surface for size measurement (maximum test diameter).

Biological patterns observed from band transect data as well as physical data (see *Results: Physical component*)

indicated that the northern and southern halves of the La Jolla kelp forest were distinct. Therefore, urchin size data for both species were divided into northern and southern groups for analysis to determine whether urchin recruitment patterns were also distinct. The boundary was located where the kelp forest narrows (see Fig. 1) because temperature data indicated these areas were subjected to different temperature regimes and because of the greater persistence of canopy in the southern half (see *Results: Physical component*). Size data for the northern and southern groups were summarized for each species using smoothed size frequency distributions (Gaussian kernel density estimator; Silverman 1986). Bandwidths were selected separately for each species and spatial group using biased cross-validation (Venables and Ripley 1999). The proportion of red urchins ≤35 mm and purple urchins ≤25 mm (first year class for each species) were then compared among the northern and southern groups to estimate spatial recruitment patterns within the forest using a bootstrap test (Efron and Tibshirani 1993). Bootstrap distributions of differences between the proportion of sea urchins with test diameters ≤35 mm for red urchins and ≤25 mm for purple urchins for pairs of sites were constructed from 2000 bootstrap samples of the data obtained by resampling with replacement sea urchin sizes pooled within the northern and southern groups. For each of the comparisons, an achieved significance level (ASL) of the test (i.e., statistical test) was computed as the proportion of bootstrap differences greater than or equal to the observed difference.

Reserve design algorithm.—The algorithm calculates an index of reserve value (RV) that we define as the relative value of protecting a particular area based on its size, the habitats located within it, the affinities of exploited species to these habitats, and individual species mobility. Specifically, each band transect within the kelp forest was discriminated into one of five habitats from the cluster analysis. The relative affinity of an exploited species to each of the five habitats was calculated as the proportional density for that species among the habitats. Some species have markedly different affinities among habitats while others are distributed more evenly among the habitats. Affinities were then used in the algorithm as weights along with species mobility weights to calculate RV for the inclusive set of twenty exploited species. The spatial units used in the calculation of RV were the 250-m boxes used to stratify the transect sampling.

The approach used in the algorithm was to build a hypothetical reserve beginning at a randomly chosen box, calculate reserve value for that box and then add to the reserve box by box in a random but contiguous fashion until the reserve encompassed the entire kelp forest. At each increase in reserve size, RV is recalculated for each box at each growth step because increasingly mobile species are afforded effective protection with increasing reserve size. Reserve values are

TABLE 1. Exploited species and reserve size threshold weights used in the analysis of reserve value (RV).

		Size threshold weight	
Scientific name	Common name	0.5	1.0
Crassedoma giganteum†	rock scallop	NA	1
Haliotis corrugata[1]	pink abalone	1	2
Haliotis rufescens[2]	red abalone	2	3
Strongylocentrotus franciscanus[3,4,5]	red sea urchin	2	4
Parastichopus parvimensis[6,7,8]	warty sea cucumber	2	4
Megastrae undosa[9]	wavy tops	2	4
Megathura crenulata[10]	giant keyhole limpet	2	4
Panulirus interruptus[5,11,12]	lobsters	3	6
Octopus spp.[13]	octopus	3	6
Paralabrax nebulifer[14]	barred sand bass	75	100
Paralabrax clathratus[15,16,17,18]	kelp bass	15	25
Sebastes atrovirens[19]	kelp rockfish	10	20
Sebastes carnatus[20]	gopher rockfish	10	20
Scorpaenichthys marmoratus[21]	cabezon	5	15
Ophiodon elongatus[22,23]	lingcod	15	25
Scorpaena guttata[19]	sculpin	100	NA
Sebastes serriceps[24,25]	treefish	5	15
Semicossyphus pulcher[26,27]	California sheephead	2	4
Sebastes caurinus[28,29]	copper rockfish	30	50
Sebastes auriculatus[28,29]	brown rockfish	30	50

Notes: The numbers below the 0.5 and 1.0 weights indicate the minimum size of the reserve in boxes (250 × 250 m) for each weight to be used in the analysis. For example, rock scallops are sessile and are therefore fully protected within one box, whereas pink abalone are potentially fully protected within one box due to limited mobility, but are considered fully protected in a reserve that is at least two boxes in size. Sculpins are not likely protected even if the entire kelp forest is protected because this species is highly mobile. "NA" indicates "not applicable." Superscript numbers in column 1 refer to sources: 1, Tutschulte (1976); 2, Ault and DeMartini (1987); 3, Mattison et al. (1977); 4, Tuya et al. (2000); 5, Parnell et al. (2005); 6, Yingst (1982); 7, DaSilva et al. (1986); 8, Shroeter et al. (2001); 9, Alfaro and Carpenter (1999); 10, P. Dayton (*unpublished data*); 11, Stull (1991); 12, Diaz Arredondo and Guzman del Proo (1995); 13, Lang (1991); 14, California Department of Fish and Game (2001); 15, Johnson et al. (1994); 16, Hartney (1996); 17, Lowe et al. (2003); 18, Cartamil et al. (2003); 19, Hartmann (1987); 20, Matthews (1985); 21, O'Connell (1953); 22, Matthews (1992); 23, Yamanaka and Richards (1993); 24, Hallacher (1977); 25, Love (1978); 26, Johnson et al (1994); 27, Topping et al. (2005); 28, Matthews (1990*a*); 29, Matthews (1990*b*).

  † Sessile.

then averaged over the boxes to calculate an average reserve value ($\overline{\text{RV}}$) for the reserve given its present size. The optimal size of the reserve can then be determined from a plot of $\overline{\text{RV}}$ as a function of reserve size. The optimal reserve size is the size where average reserve value approaches an asymptote. In other words, the size beyond which $\overline{\text{RV}}$ ceases to increase substantively with increasing reserve size. The algorithm is then repeated iteratively in Monte Carlo fashion, each time beginning with a single randomly selected 250-m box. The relationship between $\overline{\text{RV}}$ and reserve size is generally unique among iterations because each reserve is built randomly using a random seed and RV is based on the spatial distribution of habitats (identified from transect data) within the kelp forest. The result is a frequency distribution of optimal reserve sizes, each iteration contributing one value of optimal $\overline{\text{RV}}$. The mode of this distribution then represents an optimal reserve size for the area under consideration.

One important caveat to our approach is that habitat affinities may be affected by harvesting. It is not unreasonable to assume that most of the harvest by recreational and commercial fishers is taken by skilled fishers who know the locations of habitats that are important for their targeted species. This could lead to an underestimate of habitat affinity in the habitats that

are most important to particular species. This is impossible to determine without landings data collected at fine spatial scales, which are not collected in California. Underestimates of habitat affinity are most likely for the most heavily fished species. The effects of exploitation could also indirectly change the algal compositions of the habitats via a trophic cascade (e.g., see Lafferty 2004). Both issues should be addressed in the future as new large reserves are established where there will likely be enough comparable habitat in protected and unprotected areas that would enable comparisons of habitat affinities.

Calculation of reserve value.—Reserve value is calculated as follows. Each box contains multiple transects and each transect is assigned a habitat according to the results of the cluster analysis. Let h ($h = 1, \ldots, N$) represent the N habitats resulting from the cluster analysis, s ($s = 1, \ldots, S$) represent the S targeted species, D_{sh} equal the density of species s in habitat h. Then F_{sh}, the affinity of species s for habitat h is calculated as

$$F_{sh} = \frac{D_{sh}}{\sum_{h=1}^{N} D_{sh}}. \tag{1}$$

Thus, F_{sh} is the standardized density of species s among

TABLE 2. Importance of habitat-forming features for the habitats discriminated using divisive clustering analysis.

Habitat and importance	Substrate	Algae
Red turf reefs		
1°	reefs	*Egregia menziesii, Eisenia arborea, Cystoseira osmundacea*, red turf algae, articulated corallines
2°	sand, var(depth), sharp relief, ledges, crevices, overhangs	*Laminaria farlowii*
Red sea urchin reefs		
1°	bedrock, rock, var(depth), sharp relief, overhangs	*Agarum fimbriatum, Desmerestia ligulata*, brown turf algae
2°	reefs, crevices	†
Cobble gardens		
1°	cobble, sand	†
2°	†	*Pterygophora californica*
Canopy gardens		
1°	crevices	*Macrocystis pyrifera*, crustose coralline algae
2°	bedrock, bedrock lightly dusted with sand (<0.5 cm), reefs, ledges	†
Understory gardens		
1°	bedrock lightly dusted with sand (<0.5 cm), bedrock with sand cover (>0.5 cm), ledges	*P. californica, L. farlowii*
2°	†	*D. ligulata*, articulated coralline algae

Note: Primary (1°) variates were those that were greatest in that particular habitat among all habitats, and secondary (2°) variates were those whose values were at least 75% of the greatest observed value among all habitats.

† No primary or secondary habitat characteristic.

the N habitats. Reserve value is then calculated for each transect RV_{tr} in the present box as follows:

$$RV_{tr} = \sum_{s=1}^{S} F_{sh} w_{sb} \quad (2)$$

where w_{sb} is the species mobility weight for species s given the number of boxes in the present reserve b. The mobility weight w_{sb} depends on the number boxes required to protect each species based on home range information from the literature. For the present study, we used weights of 0, 0.5, and 1 (see Table 1). A weight of zero was assigned to species whose ambits were clearly larger than b because those species could not possibly be protected by a reserve of size b. A weight of 0.5 was used for species whose ambits are such that they might be protected in a reserve of size b. And species whose ambits were smaller than b were assigned a weight of 1 because they are fully protected by a reserve of size b. Reserve value for each box, RV_{box}, was then calculated as

$$RV_{box} = \frac{\sum_{tr=1}^{TR} RV_{tr}}{TR} \quad (3)$$

where TR is the number of transects conducted in box. Average reserve value for the reserve of iteration i for the number of boxes b is then

$$\overline{RV}_{ib} = \frac{\sum_{box=1}^{b} RV_{box}}{b}. \quad (4)$$

An optimal size was determined for each iteration as the reserve area A where $\overline{RV}_{ib}$ was asymptotic beyond the size that achieved at least 75% of the reserve value when the entire forest RV_B is protected, where B is the total number of boxes in the forest. The 75% threshold is subjective and, in this case, was based on the observation that the relationship $\overline{RV}_{ib}$ (A) exhibited asymptotic behavior in the majority of iterations where $\overline{RV}_{ib}$ was at least 75% of RV_B. Optimal reserve sizes from each iteration were then pooled to form a distribution from which the mode was used to determine the optimal size for a reserve in the kelp forest off La Jolla.

Home range areas were used for size threshold weights, w_{sb} when available. For species whose home range areas were not available, weights were determined in two different ways. First, area was calculated from linear distance for species whose home range estimates were given as linear distances. For species whose home ranges were not available, weights were chosen based on the minimum size of a reserve that had been shown to effectively protect that species.

Simplifying reserve boundaries.—The next step was to determine the reserve location that maximizes $\overline{RV}$ based on optimal size. For practical reasons, the boundaries of a reserve must be simple. Therefore, we modified the algorithm to calculate $\overline{RV}$ based on boundaries normal to shore. The procedure was to calculate $\overline{RV}$ using the sampling grid rows. $\overline{RV}$ was calculated for a reserve whose northern boundary was the northernmost row and whose southern boundary was set by the requirement that the reserve had to protect at least the optimal number of boxes without including the next southern row. This procedure was repeated progressing from north to south until the southernmost row was included.
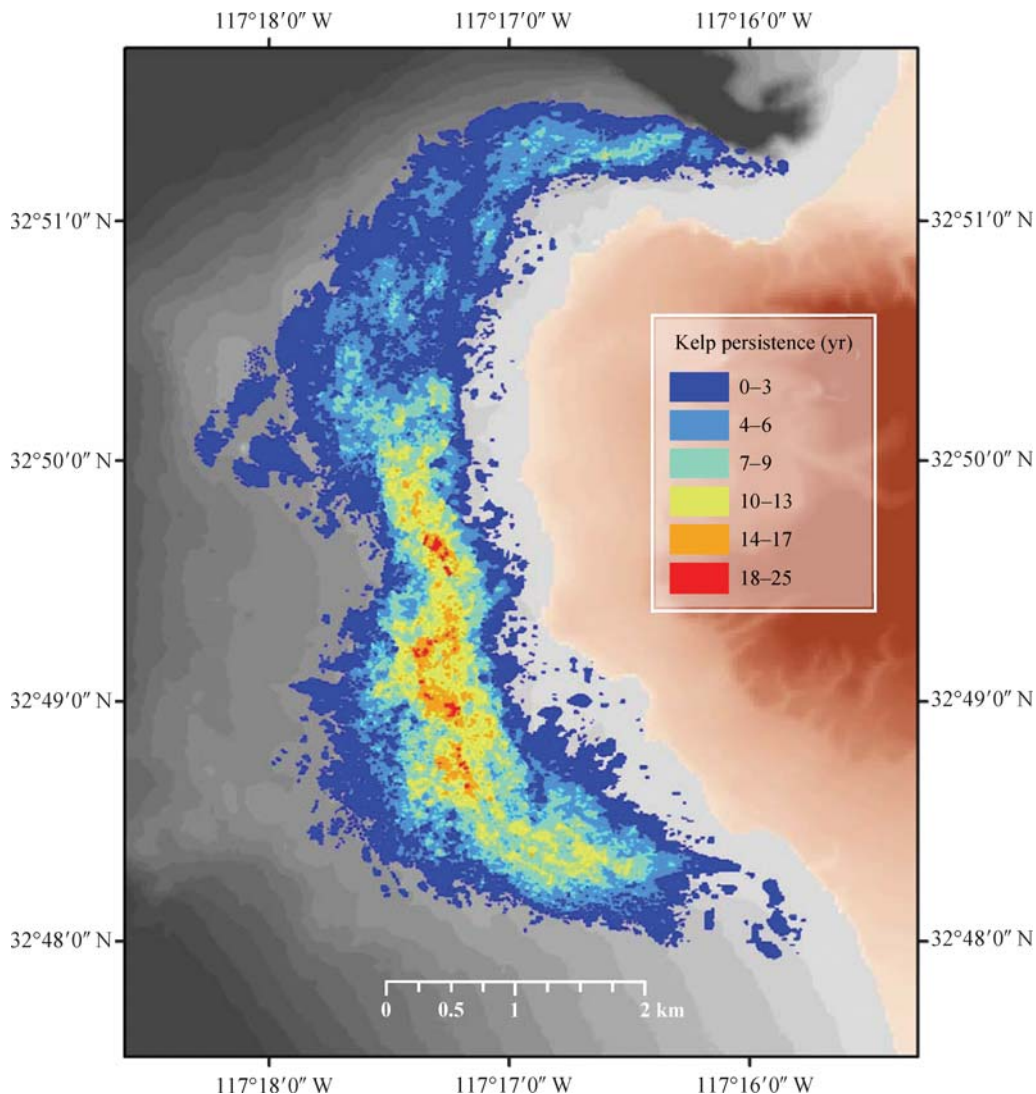
Fig. 2. Map of La Jolla kelp forest showing spatial distribution of kelp persistence in years from 1967 to 1999 (data from Ocean Imaging, Inc., Solana Beach, California, USA).

The result is a graph of $\overline{RV}$ as a function of reserve location.

Historical data.—Historical data and information regarding the condition of the kelp forest over the last ~50 years and urchin size frequencies were available from archived notes and data of former Scripps researchers W. North, C. Limbaugh, and J. Quast. The spatial distribution and area of kelp canopy for the period 1967–2002, determined from aerial photographs (see North et al. 1991 for details) was obtained from Ocean Imaging Corporation (Solana Beach, California, USA) in GIS format.

Physical component

Temperature.—Bottom temperatures were sampled at six locations near the kelp forest (Fig. 1) to determine the spatial distribution of temperature. Thermistor strings were deployed near sites C22 and E22 with sensors at 0.5 and 2 m above the bottom, and 8 and 1 m below the surface. Bottom temperatures were sampled at 10-min intervals from June 2002 to February 2003 and April 2004 to January 2005. Thermistor string data were collected from September 2003 to December 2004 at 4-min intervals. Tidbits (Onset Computer, Bourne, Massachusetts, USA) were used for all temperature measurements.

Currents.—Currents were measured at two locations near the kelp forest (Fig. 1). Currents were measured simultaneously at both sites using bottom-mounted acoustic doppler current profilers (ADCPs; RDI Workhorse, 600kHz; RDI Instruments, San Diego, California, USA). The instruments were ~25 m deep and sampled in 1-m depth bins. Current meters were deployed when available (27 October to 14 November

2003 and 14 May to 30 May 2004). Current magnitudes in all depth bins deeper than 5 m were pooled within sites and compared among sites (northern vs. southern) using a *t* test (Sokal and Rohlf 1981). Current data from bins shallower than 5 m were subject to periods when the signal to noise ratio was low, therefore these depths were not used in the comparison analysis.

Wave energy.—Wave exposure is an important factor that affects and defines habitat, and is therefore an important consideration for reserve design. Output from a coastal model of wave refraction–diffraction off San Diego (see O'Reilly and Guza 1993) was used to develop spatial maps of significant swell heights along the 10-m contour off La Jolla for 2002 and 2003. Wave energies were then calculated from significant wave heights to generate spatial maps of mean and maximum daily wave energy of 100 m long segments along the 10-m contour to produce a time-averaged map of wave energy.

RESULTS

Historical patterns

Kelp coverage in La Jolla has been extremely dynamic over the period that reliable data are available beginning in 1946 (Fig. A1). This is true for all kelp forests of southern California (North et al. 1991) and is primarily forced by storms and nutrient stress associated with climatic cycles such as ENSO and the Pacific Decadal Oscillation (PDO), and fluctuations in population size and foraging behavior of sea urchins, which are important kelp grazers (Dayton et al. 1992). During the late 1940s and early 1950s, the kelp forest was in "historically poor shape" (W. North, *unpublished notes*). There was some recovery by the mid-1950s, but El Niño conditions persisted from 1957 to 1959, when there was a prolonged period of warm water and three catastrophic storms causing widespread giant kelp mortality. This was followed by a prolonged period of severe urchin grazing, which although widespread throughout La Jolla, was worse in the northern half of the forest. Comparison of data gathered in 1964 (W. North, *unpublished data*) and our surveys reveal that purple and white sea urchins, *Lytechinus anamesus*, were much more abundant than they are now (Fig. A2), while red sea urchins were slightly more abundant. White sea urchin densities averaged ~5.7 m² in 1964, but presently are very rare. Only two white urchins were observed throughout La Jolla during our survey throughout the forest. The spatial distribution of the kelp forest off La Jolla has also been dynamic (Fig. 2). Since 1967, aerial photographic data indicate that the southern half of the kelp forest has been much more persistent despite intensive replanting and quickliming (where quicklime is applied to the bottom to kill sea urchins) efforts in the 1960s and 1970s. Though not as quantitative as aerial photographs (W. North, *archived notes*; North et al. 1991) observed that this pattern began after the extended El Niño of 1957–1959, when canopy disap-

peared in the northern half while some persisted in the southern half.

Biological component

Kelp habitats.—A total of 286 band transects were conducted in kelp forest habitats. Divisive clustering analysis yielded five major types of habitat that were separated by robust splits (see Parnell et al. 2005). The major characteristics of these habitats are listed in Table 2. Habitat types were named according to their major characteristics. The primary habitats included (1) red turf reefs, (2) red sea urchin reefs, (3) cobble gardens, (4) canopy gardens, and (5) understory gardens.

The spatial distribution of the habitats is shown in Fig. 3. Habitats in the northern half of the forest were more diverse than the southern half where they consisted mainly of canopy gardens and red sea urchin reefs. The northern half was predominantly a mixture of red turf reefs, red sea urchin reefs, understory gardens, and canopy gardens. Cobble gardens were limited mainly to the central section of the forest where the forest is narrowest. Divisive clustering analysis was also conducted using only bottom characteristics and excluding algal data. The result was four distinctive clusters that were distributed similarly among both halves of the forests indicating that bottom composition and structure is not different among the two halves.

Relative affinities of exploited species within these habitats, based on densities (F_{sh}), are listed in Table 3. The last row of Table 3 lists the proportional affinities of these species by habitat as an indicator of habitat utility for the collective set of exploited species. Affinities for red sea urchin reefs and canopy gardens appear to be the best habitat for this combined set of species. Species affinities to red turf reefs is a third less, while affinities to understory gardens and cobble gardens are substantially less. In fact, understory gardens were poor habitats for all species, not just exploited species. The breadth of habitat utilization by each species is shown in Fig. 4. Red abalone, lingcod, and rockfish exhibited the narrowest habitat breadth while species such as barred sand bass, sheephead, and wavy turbans appeared to be generalists. Wavy turbans occupied the five habitats nearly equally. The results of the BIO-ENV analysis indicate that habitat for the set of exploited species was partly defined by reefs, rocks, red turf algae, crustose coralline algae, and average relief. These parameters accounted for ~36% of the variance observed in the set of exploited species. Of these parameters, rocks, crustose coralline algae, and average relief were the most important parameters since they were included in all results.

The spatial distribution of diversity is shown in Fig. 5. The highest diversity was observed in the southern edge of the forest, and in general, the diversity of the southern half was greater than the northern half. There were some areas on the outer edge of the forest in the northern half
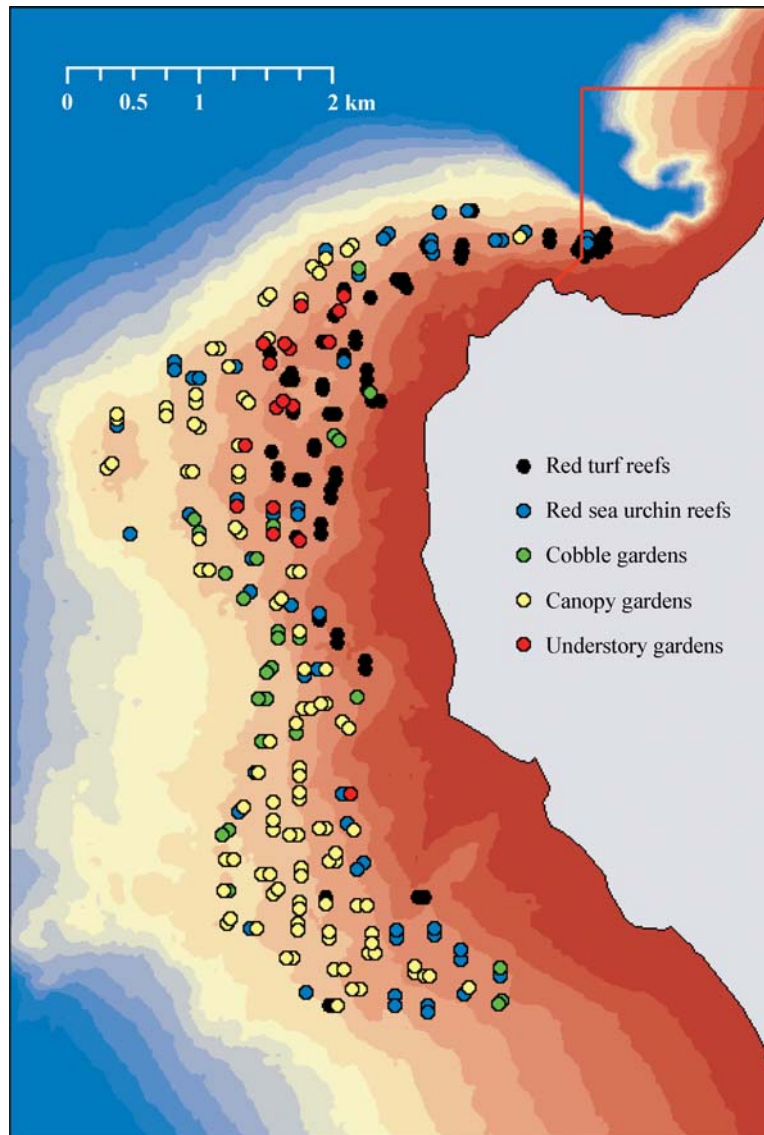
Fig. 3. Distribution of habitat types based on divisive cluster analysis of habitat parameters (see *Results: Biological component: Kelp habitats*).

with moderately high diversity. Of particular note is that diversity in the present reserve is low.

Urchin size frequencies.—Differences in the size frequency distributions between the northern and southern halves of the forest (Fig. A3) were highly significant (ASL < 0.001) for both species. The observed difference in the proportion of sea urchins making up the first-year class between the northern and southern halves was ~5% for red sea urchins, and ~6% for purple sea urchins in the northern half.

Analysis of reserve value (ARV).—Results from an individual run of the analysis of reserve value are shown in Fig. 6. The black box in the figure was the seed for this particular run and colors correspond to mean reserve value ($\overline{RV}_{ib}$), which increases (upper right figure)

as the reserve grows. The variance of $\overline{RV}_{ib}$ also increases due to the addition of different habitats having different reserve values. The median value for the size of an optimal reserve in the forest off La Jolla was 53 boxes (~3.3 km^2; based on 2000 runs). The entire forest comprises 128 boxes, therefore an optimal reserve should include ~42% of the forest.

The optimal location for a reserve of 53 boxes was then determined by moving the boundaries of the reserve to maximize $\overline{RV}_{ib}$. The results are shown in Fig. 7. Reserve value is maximal when the northernmost boundary of the reserve is the top of row 15, and the reserve extends to the southern end of the kelp forest (bottom of row 25). This reserve would protect 55 boxes (~3.4 km^2), approximately 43% of the kelp forest.

TABLE 3. Standardized habitat affinities (F_{sh}) of fished species to five types of habitat within the La Jolla kelp forest.

Common name	Red turf reefs	Red sea urchin reefs	Cobble gardens	Canopy gardens	Understory gardens
Kelp bass	0.357	0.242	0.041	0.164	0.195
Barred sand bass	0.204	0.232	0.064	0.262	0.237
Sheephead	0.205	0.261	0.101	0.211	0.222
Sculpin	0.273	0.345	0.000	0.293	0.090
Cabezon	0.126	0.238	0.084	0.304	0.248
Lingcod	0.000	0.495	0.000	0.505	0.000
Kelp rockfish	0.107	0.417	0.119	0.287	0.070
Copper rockfish	0.094	0.358	0.000	0.547	0.000
Gopher rockfish	0.163	0.448	0.073	0.316	0.000
Brown rockfish	0.190	0.401	0.000	0.409	0.000
Treefish	0.121	0.427	0.065	0.388	0.000
Rock scallops	0.222	0.444	0.000	0.334	0.000
Pink abalone	0.391	0.214	0.067	0.226	0.102
Red abalone	0.159	0.000	0.000	0.841	0.000
Octopus	0.247	0.241	0.328	0.184	0.000
Red sea urchins	0.215	0.308	0.089	0.276	0.112
Warty cucumber	0.187	0.344	0.035	0.278	0.156
Wavy turbans	0.217	0.185	0.156	0.211	0.231
Giant keyhole limpet	0.153	0.289	0.083	0.299	0.175
Lobster	0.347	0.308	0.058	0.216	0.070
Proportional affinity	0.199	0.310	0.068	0.328	0.095

Notes: Proportional habitat affinities for the combined set of species are shown in the bottom row. The proportional habitat affinity for all species combined is the frequency of all exploited species among the habitats.

Physical component

Temperature.—The primary temperature pattern was of decreasing average temperatures from north to south (Fig. 8). The difference between the means of the northernmost and southernmost stations was ~1.1°C. A dominant pattern in the time series included 2–7 d events in which temperatures substantially cooled or warmed throughout much of the forest and 1–3 d periods in which the northern half of the forest was warmer (up to 2°C) than the southern half (e.g., Fig. A4). Temperature variability was ~10% higher in the northern half. Data from thermistor strings located near sites C22 and E22 indicated that near bottom internal wave activity was greater in the north, while in the south bottom sensors were below the depth of tidally generated internal waves. As a result, the benthic zone in the southern forest is more frequently bathed by cool bottom water than the north.

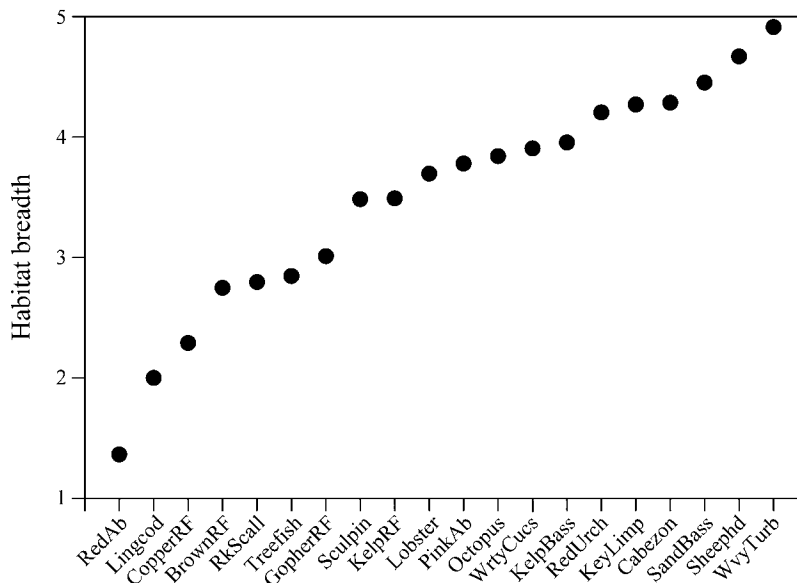*Currents.*—Currents observed during both ADCP

FIG. 4. Habitat breadth of exploited species within the La Jolla kelp forest (see Table 1 for full species names). Habitat breadth is a measure of how many habitats, on average, each species occupies. Habitats (five) were derived from divisive clustering analysis (see *Results: Biological component: Kelp habitats*).
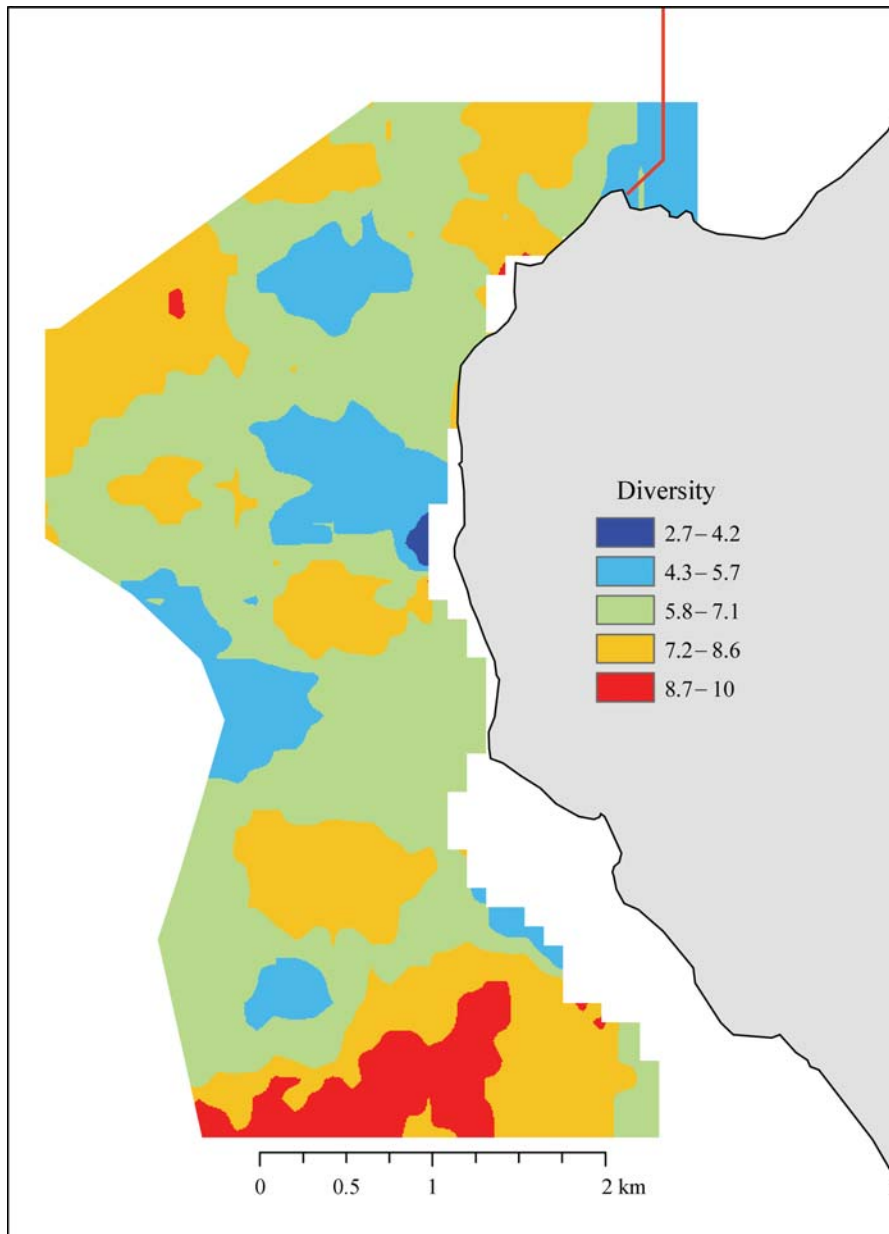
Fig. 5. Spatial distribution of diversity (Hill's $N1$) in the La Jolla kelp forest. All surveyed species (61) were included in the analysis.

deployment periods were similar. Major axes for currents throughout the water column at both sites were oriented WSW to ENE at all depths (Fig. A5). This orientation is predominantly cross-shore for most of the kelp forest, with the exception of the far northern area. However, minor axes for near surface currents were nearly as large as major axes due to the predominant northwest diurnal sea breeze. Both tidal and subintertial currents were uncorrelated between the southern and northern sites, with the exception of the wind-influenced near-surface currents, even when directional components were rotated to align with the shore or bathy-

metry. This indicates that currents in the northern and southern halves of the forest are subjected to different local forcing and that the circulation off La Jolla is complex. This is exemplified by observed tidal frequencies at both sites. The dominant tidal frequencies at the northern site are the diurnal K1 (luni-solar diurnal) and semidiurnal M2 (principal lunar) tides, while the dominant frequencies at the southern site are diurnal tides K1 and O1 (principal lunar diurnal). This may be the result of local topography, which is considerably different between the northern and southern ends of the headland. Average current magnitudes decrease from

the surface to bottom at both stations. Overall, current magnitudes between 5 m and the bottom (25 m) are significantly greater ($P < 0.003$) at the northern site compared to the southern site. Current magnitudes in the middle of the water column at the northern station were particularly stronger (35%) than the southern station. This pattern is also typical of flow around a headland, where current magnitudes are greatest just off the tip (Geyer 1993).

Wave energy.—The distribution of wave energy along the length of the kelp forest appeared to be spatially symmetrical around the middle of the forest since the shape of the bottom in the northern and southern halves are strikingly similar. The spatial pattern of wave exposure was also similar among the halves during extreme events (days when the average of wave heights for the entire length of La Jolla were greater than the 95th percentile; see Fig. A6).

Discussion

The process of reserve design must be scientifically defensible and transparent in order to maximize potential effectiveness and the likelihood of establishment. In marine reserve design, there is an inherent continuum of uncertainty. Habitat quality and distribution represent the most certain factors, while factors such as ecological links to nearby or remote habitats (e.g., adult migration and larval dispersal), while of critical importance (e.g., Sala et al. 2002, Largier 2003), are more difficult to measure and therefore less certain. Our proposed reserve in La Jolla is primarily based on the types, quality, and distribution of habitats as well as the relative value of these habitats to our set of exploited species. The quality and distribution of habitats off La Jolla appear to be affected by the oceanographic climate, which differs between the northern and southern areas. This spatial pattern of oceanographic climate coincides well with the distribution of habitats we observed and their stability through time. The different forcing observed between these areas may also determine important differences in larval retention and the connective capacity with other similar habitats. Our results indicate the importance of fine-scale approaches to adequately define habitats and determine habitat value for exploited species in marine reserve design.

Habitats and diversity

The importance of habitat for the definition of coastal reserves is obvious. However, habitat definitions are often coarsely defined (e.g., "hard" vs. "soft" bottoms). Clearly, there is a tradeoff between geographical scope and fine-scale habitat resolution. The question is how much fine-scale resolution is necessary for reserve design. This is an important question because naturalists know that habitat requirements can be extremely variable among species and tend to be idiosyncratic. In our case, there are clearly different habitats (subhabitats) within kelp forests, and each kelp forest is likely

unique with regard to the area and spatial arrangement of these habitats. Because species have varying affinities to subhabitats, we determined the distinctive types of subhabitats within the La Jolla kelp forest and the affinities of exploited species to these subhabitats to determine an optimal reserve that includes enough of the most important subhabitats to protect the set of exploited species during their adult (exploited) phase while closing as little area as possible.

Our results indicate a large-scale pattern of subhabitats and diversity in the kelp forest with a more even distribution of habitats in the north yet greater species diversity in the south. The overall pattern of diversity is linked to the distribution of subhabitats because diversity significantly differs among subhabitats (Fig. A7; one-way ANOVA, $P < 0.001$). The north is more a mix of habitats than the south, which is dominated by the subhabitats with the highest diversities, canopy gardens and red sea urchin reefs. A cursory examination of habitat pattern without information on the diversity of these subhabitats would lend support for protecting the northern area since inclusion of a broad range of habitats is a goal for reserve design to protect ecosystem function (Roberts et al. 1993). However, such a reserve would fail to protect the most diverse areas of the forest, which because of their diversity, are more critical for ecosystem function.

The pattern of diversity discussed above is based on all 61 species of fish and invertebrates that we studied, but is it relevant to the 20 species that are exploited by commercial and recreational fishers? Fig. 4 indicates that the importance of these subhabitats varies among the exploited species. The subhabitats are very important for species such as red abalone, lingcod, and rockfish but are less relevant for the more ubiquitous species such as sheephead and wavy turbans. Thus our subhabitats are an important consideration for marine reserve design. The analysis of reserve value discussed later incorporates habitat specificity for the entire set of exploited species to determine an optimal reserve size and location off La Jolla.

Physical forcing and habitat distribution

The distribution and stability of the subhabitats we observed off La Jolla appear to be influenced by ocean microclimate (temperature and currents) since the spatial patterns of canopy stability, subhabitats, and ocean microclimate appear concordant. The temperature regimes between the northern and southern halves are clearly different with chronically cooler temperatures and a shallower thermocline (i.e., internal wave interface) in the southern forest. Currents are also different between the two areas, with mean current magnitudes significantly greater throughout much of the water column in the north. The possible effects of differential temperatures and current on the kelp forest are discussed below. Other physical factors known to affect algal community structure include wave energy (Harrold et al. 1988,
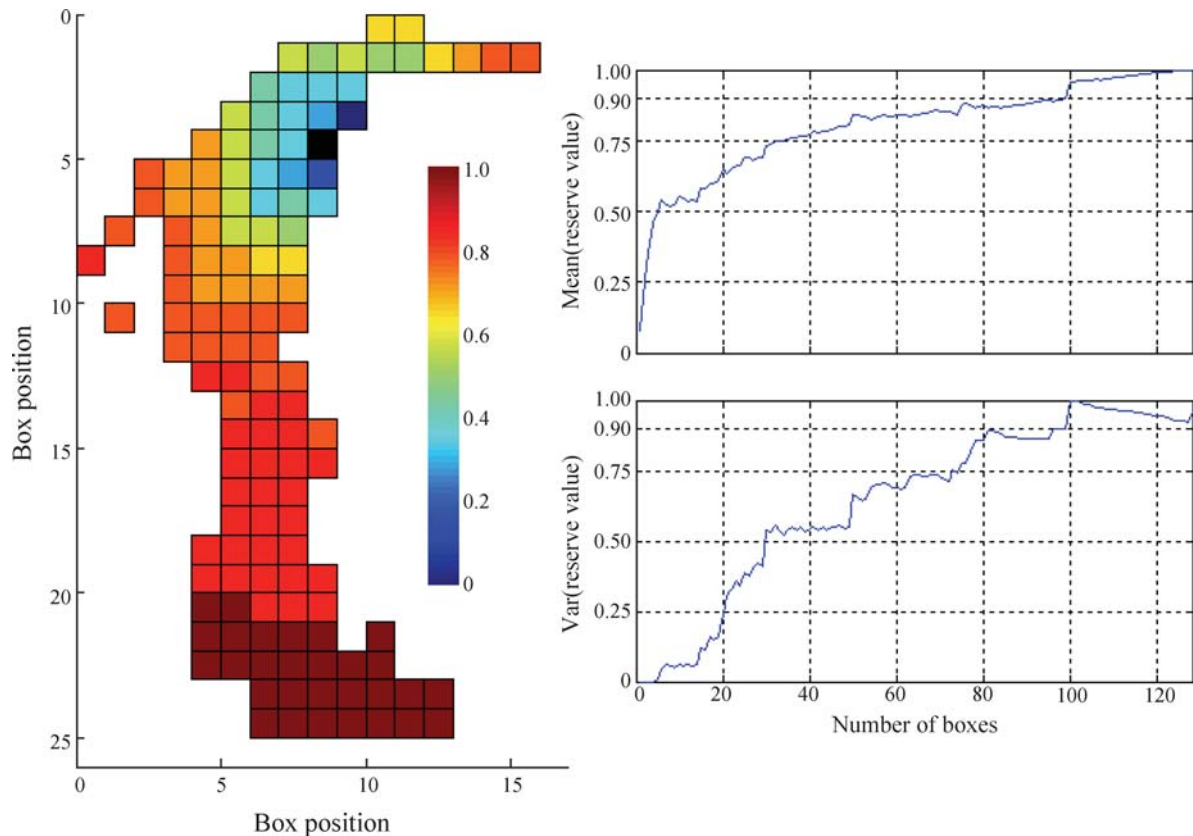
FIG. 6. Sample output of one run of the reserve analysis algorithm. The plot at left indicates the spatial distribution of mean reserve value (RV) as the reserve grows from a random seed box (black box). Colors indicate increasing mean reserve value (key, bottom to top). On the right, the top graph is the normalized mean value of the reserve as it grows, starting from a single box; the bottom graph is normalized variance of reserve value. Box size is 250×250 m.

Graham et al. 1997, Duggins et al. 2003) and bottom shapes and composition (North 1994). These factors are not likely responsible for the spatial pattern of sub-habitats we observed off La Jolla because their spatial distributions were similar in both halves of the forest.

Temperatures in the southern half appear less variable and cooler, indicating chronically higher nutrient conditions in the south. The negative relationship between kelp nutrient concentrations (NO_3) and temperature is well established for waters off southern California (Zimmerman and Kremer 1984) and the importance of nutrient forcing on kelp communities is well documented (Dayton et al. 1999). A deeper thermocline limits nutrient availability for *Macrocystis pyrifera* because most of the nutrient-absorbing surface area of *M. pyrifera* is in the upper part of the water column (Jackson 1977). Understory kelps on the other hand are less frequently exposed to low nutrient concentrations because these kelps do not extend far above the bottom. The general result of a deeper thermocline is that giant kelp is nutrient limited relative to understory kelps. Further, warmer bottom temperatures can result in reduced recruitment of giant kelp (Dayton et al. 1984). For La Jolla, this means that conditions for growth and

recruitment of giant kelp in northern La Jolla are less amenable than the southern forest. The spatial pattern of mean temperature and percent cover of giant kelp per unit of hardbottom appear related (Fig. 9). The different temperature regimes of the northern and southern areas may also be important in determining patterns of kelp community responses to El Niño (North 1991). Cooler temperatures and a shallower thermocline in the south would tend to reduce the effects of El Niño there and hasten recovery rates. As early as the 1950s, North (1991) observed that biological patterns off La Jolla indicated the northern part of the kelp forest is likely warmer.

The circulation off La Jolla may indirectly affect the kelp communities of the two halves of the forest by the differential larval flux of kelp herbivores such as sea urchins. Given similar larval concentrations, an area exposed to higher currents receives a greater input of larvae for recruitment. This may be the case for northern La Jolla where current magnitudes are greater, and would account for the significantly higher rates of purple and red sea urchin recruitment we observed in the north. Such a pattern is somewhat self-reinforcing because greater sea urchin recruitment in the north increases the
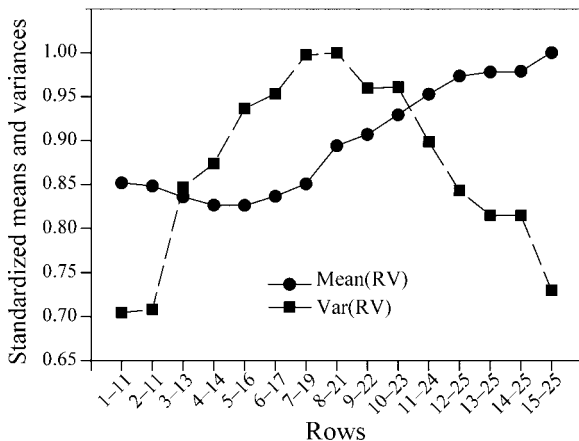
FIG. 7. Standardized means and variances of $\overline{RV}_{ib}$ (average reserve value for the reserve of iteration i for the number of boxes b) of a reserve protecting at least 53 boxes ($\sim$3.3 km^2) moving north to south within the kelp forest. The graph was used to determine simplified latitudinal (row) boundaries for a reserve off La Jolla. The abscissa shows the row boundaries for possible reserves containing at least 53 boxes. $\overline{RV}_{ib}$ is maximal for a reserve including the area between rows 15 and 25. $\overline{RV}_{ib}$ is less for the three reserves whose northernmost row is north of row 15 (i.e., 12–25, 13–25, and 14–25 on the abscissa) because the affinities of exploited species to the habitats in rows 12, 13, and 14 are less than those for row 15.

FIG. 9. Relationship between percent cover of *Macrocystis pyrifera* and concomitant temperature. Percent cover of giant kelp from 0.5-m line intercept data (see *Methods*) was divided by percent hardbottom (line intercept) on the same transects to standardize percent kelp cover by the amount of available hardbottom. Kelp data were spatially pooled by distance from the temperature stations. Reserve transects were not included due to the confounding effect of protection from kelp harvesting or trophic cascade effects. Temperature means and standard errors are from data from sites A22–F22. The slope obtained from a weighted linear regression of mean kelp cover on temperature was significantly different from zero ($P < 0.01$). Note, however, that the point from the northernmost (warmest) area is influential in establishing this result.

potential for overgrazing, which can result in reduced kelp canopy. Since stands of giant kelp significantly attenuate currents (Jackson and Winant 1983), reduced canopy levels in the north combined with stronger currents would lead to even higher levels of urchin recruitment. It is interesting to note that sea urchin fishers are well aware of the higher recruitment rates in the north because the northern area is the most productive for red sea urchins (P. Halmay, *personal communication*). Differences in temperature and flow regimes between the two halves of the forest are also evident in the distribution of suspension feeders such as *Muricea californica* (Fig. A8), which grow faster and have reduced mortality with increasing current speeds and which require temperatures of at least 15°C to reproduce (Grigg 1970).
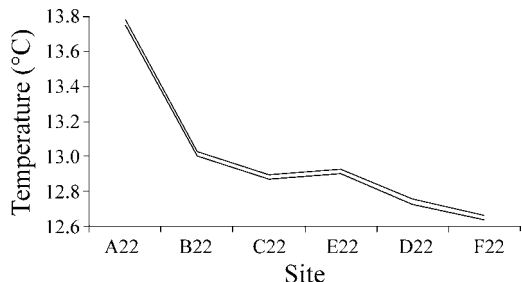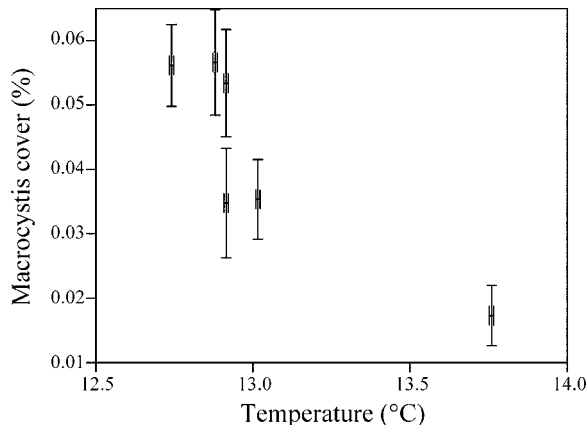

FIG. 8. The 95% CI of temperatures at stations A22–F22, shown as 95% CI of the mean. Temperature was recorded at each station at 10-min intervals during two sampling periods for a total of 65 040 samples at each station.

We also suggest that the processes described above account for the dynamics of the La Jolla kelp forest over the last half century. The condition of the canopy prior to the 1980s was dramatically reduced especially in the northern part of the forest where sea urchins were once much more abundant than they are today. Presently, the densities of both red and purple sea urchins among the two halves are not significantly different. The storms and warm water associated with the El Niño of 1982–1983 and the subsequent 200-yr storm in 1988 (Seymour et al. 1989, Dayton et al. 1992) likely ended this persistent sea urchin barren in the north due to mechanical destruction of the sea urchins and indirectly through sea urchin diseases associated with prolonged periods of warm water during the 1982–1983 El Niño. Abundant canopy did not develop in the north until after the 1982–1983 El Niño. In summary, we suggest that the kelp community in the north is more dynamic and has more understory because it is exposed to a lower and more variable nutrient climate than the south, a pattern that is exacerbated during El Niño conditions (Tegner and Dayton 1991). In addition, the northern area likely receives a greater input of sea urchin larvae. While we do not have mechanistic data to support these arguments, they represent the most likely cause of the patterns we observe based on known kelp forest ecological processes. The fact that areas of a single kelp forest likely respond differently to external perturbations due to differences in temperature and circulation patterns on such a small scale attests to the inherent

resiliency of the system and merits further study. Complex, small-scale circulation near headlands is also likely to increase the dispersal and retention of larvae by increasing the length of the path traversed while larvae are in their planktonic stage (Okubo and Levin 2002). Larval retention in eddies formed by headlands have been observed in the lee of islands (Swearer et al. 1999), but small-scale effects are not well understood. Future work is planned to further discriminate the effects of physical forcing on the stand of giant kelp and the larval climate off the La Jolla headland.

The biological patterns we have observed within the La Jolla kelp forest result from both biological and physical processes. We are proposing that the different ocean climates between the two halves of the forest make it likely that the same algal communities will repeatedly develop after large-scale disturbances that wipe out much of the kelp forest. However, the degree to which this is true is tempered somewhat by the large predators and other species that have been depleted by humans over the past century. These species could indirectly affect the algal stand, and therefore the fine-scale habitats. We have observed the kelp forests of southern California only during this depleted "shifted-baseline" period. Therefore, the degree to which the recovery of these important species has on the habitats of the La Jolla kelp forest after a large reserve is established is not known.

Analysis of reserve value

There are several recent approaches to evaluating the potential value of reserve designs. One of the most promising combines the scientific and social factors that integrate the protection of ecosystem structure and function (Jones 2002). Our approach facilitates such an integrated evaluation because the resulting reserve is located and sized in a strictly quantitative manner based on habitats and species mobility, thereby achieving adequate protection of critical structure while closing a minimum of area. The analysis of reserve value (ARV) was developed with these priorities in mind.

Our method differs fundamentally from other reserve siting algorithms in which reserves are designed with predetermined conservation goals in mind such as fixed percentages of habitat (Airame et al. 2003, Leslie et al. 2003), fixed percentages of spatially explicit biomass (Meester et al. 2004), or targeted percentages of biodiversity (Ward et al. 1999, Possingham et al. 2000). In contrast, our algorithm does not estimate an optimal reserve size based on a priori targeted percentages of habitat, biomass or biodiversity. Rather, our method estimates the area that is required to optimize the value of the reserve to our set of exploited species based on (1) fine-scale habitats, (2) the value of these habitats to the exploited species, and (3) the postlarval mobility of these exploited species.

In our application of ARV in La Jolla, we calculate $\overline{RV}$ in a linear fashion despite the fact that $\overline{RV}$ may respond nonlinearly to increasing reserve size. However, the amount of information to determine nonlinearity is much greater than is presently available because responses of individual species to increasing reserve size would have to be determined experimentally.

Inspection of individual iterations reveals that $\overline{RV}$ quickly increases with increasing reserve size and then approaches an asymptote beyond which little value is gained by further enlargement of the reserve (Fig. 6, upper right panel). For La Jolla, the median value of 53 boxes generated from 2000 runs corresponds to ~85% of the value of protecting the entire kelp forest, and protection of 55 boxes from rows 15–25 of the kelp forest (see Fig. 7) achieves protection of ~97% of the value of protecting the entire forest. Therefore, extending the reserve beyond the 55 southernmost boxes is not likely to significantly increase the effectiveness of the reserve for our set of exploited species.

The approach used in ARV is generally applicable to any system at any spatial scale for any number of exploited species. The next obvious refinement would be using the algorithm for the design of reserve networks using known ecological linkages, such as a probability model of larval dispersal and adult movements among areas. The algorithm can also be slightly modified to weight species by their importance in any particular reserve.

Larval connectivity and retention

Ecological links among habitats are a critical component for the design of marine reserve networks (Sala et al. 2002). This is especially true for the design of reserve networks in southern California because rocky habitats are presently highly fragmented compared to the Pleistocene when sea level was much lower. Present rocky habitats in southern California are small and fragmented by comparison and are essentially isolated outcrops in a sea of sand compared to the relatively unbroken rocky habitats prior to the Holocene (Graham et al. 2002). Presently, there is a large-scale spatial analogue of this gradient from highly fragmented habitats to nearly continuous habitats along the range of *Macrocystis* sp. off the west coast of N. America (J. A. Estes, *personal communication*), where habitats are highly fragmented in central Baja and nearly continuous in British Columbia and Alaska. Larval connectivity among rocky habitats is critical for fragmented habitats to recover from local extirpations and for reserves to supply larvae of exploited species to similar exploited habitats. On the other hand, larval retention is critical for self-sustainment. The degree to which habitats are connected or retentive with respect to larvae is variable among species given their variable larval periods, behaviors, and the complexities of coastal circulation. Complex coastal circulation, variable larval periods, and behaviors all contribute to the difficulty of designing reserve networks. The most promising approaches are ones that are based on probabilities of larval exchange among habitats and reserves (e.g., Lockwood et al. 2002, Palumbi 2003).

The reserve that we propose is based on a fine-scale definition of the habitats and the value of these habitats to exploited species. Since our results indicate that the two halves of the forest appear to be exposed to different physical forcing, it is quite possible that these areas also differ with regard to their potential larval retention and connectivity with remote habitats and retention. Export of larvae to remote areas is enhanced by cross-shore circulation, which advects larvae away from the coastal boundary layer seaward, where dispersal through both advection and diffusion is higher (Okubo and Levin 2002, Largier 2003). On the other hand, areas with the highest cross-shore circulation are also more likely to receive larvae. Currents in both halves of the La Jolla kelp forest show evidence of complex flow patterns, including enhanced cross-shore circulation typical of circulation near headlands (Geyer and Signell 1990, Geyer 1993). This implies that the La Jolla kelp forest overall is a desirable forest for a reserve because it is both more likely to export local larvae and receive remote larvae than kelp forests located near straight coastlines where alongshore flows dominate. Greater current magnitudes in the north and more persistent flow-damping canopy in the south mean the northern area has a greater potential to receive and export larvae than the south. Whereas, weaker currents and kelp-dampened currents in the south imply the south is more likely to be retentive for larvae. However, the currents in the south are dominantly cross-shore, therefore there is still strong potential for offshore larval export in this area. Because of this and because our proposed reserve in the south provides higher quality adult habitat (cf. stock habitat) than the north, we suggest that the southern half of the forest is of more value as part of a network than the northern half. This supports leaving the more productive area for red sea urchins in the north open to exploitation while protecting the southern area whose capacity for self-sustainment is greater due to dampened flow and habitat stability.

Rather than expanding the present reserve, the establishment of a reserve in the southern portion of the forest would also be more acceptable to commercial lobster fishermen and recreational fishermen. The distribution of fishing effort for lobsters is greater in the northern half than the southern half (P. E. Parnell, *unpublished data*), and the area off the northwest tip of the forest is an area that is the favorite fishing area for commercial passenger fishing vessels (CPFVs) as well as private boaters fishing for pelagic sportsfish. The existing reserve should not be changed as it currently protects reproductively important populations of vermillion rockfish and green abalone as well as a unique submarine canyon (see Parnell et al. 2005).

Conclusions

We have presented a habitat-based scheme for designing marine reserves that calls for prioritizing certainty in reserve design by focusing on habitats, the importance of habitats to exploited species, and the resilience and stability of these habitats. We propose a "no-take" reserve within the La Jolla kelp forest that optimizes protection of critical habitat for the set of exploited species off La Jolla and the area left open to exploitation. Biological and physical patterns observed off La Jolla are highly concordant and correspond with historical patterns observed over the last fifty years suggesting that our definitions of critical habitat are robust. Our results indicate that the southern area of the kelp forest would be the best site for a reserve off La Jolla. Based on the analysis of reserve value, the boundaries of this optimal reserve are the latitudes of 32°48′00″ and 32°49′30″, and the reserve should extend offshore to the limit of contiguous hardbottom thus protecting critical kelp forest edge habitat and protecting benthic fish that forage between the offshore edge of the kelp forest and the offshore edge of rocky habitat (see the Appendix: Fig. A9).

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APPENDIX

Figures showing the time series of *Macrocystis pyrifera* canopy cover in the La Jolla kelp forest; densities of sea urchin species in 1964 and 2002; size frequency distributions of red and purple sea urchins; a surface plot of temperature for one month in 2003; variance of currents along major and minor axes at three depths; distribution of wave energy; mean diversities for habitats determined from divisive clustering analysis; spatial distribution for the gorgonian, *Muricea californica*; and a map of the proposed reserve (*Ecological Archives* A016-036-A1).