Habitat fragmentation, patch size, and the recruitment and abundance of kelp forest fishes

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ABSTRACT: Studies of habitat fragmentation in marine ecosystems are few, despite a high potential for disturbance and the fragmentation of macrophytes that constitute important habitats. In this study, we investigated the relative importance of habitat fragmentation and loss on the recruitment and abundance of fishes associated with giant kelp *Macrocystis pyrifera* forests. We experimentally fragmented naturally occurring kelp forests at 3 sites along Santa Catalina Island, California, USA, into areas of 100 to 1600 m^2. We also explored the relationship between kelp patch size and recruitment of fishes at smaller spatial scales by constructing kelp plots that were consistent in density but varied in area. The numerical and biomass densities of recruit, older juvenile, and adult fishes across fragment areas differed among species, resulting in linear, exponential, or asymptotic increases in numerical and biomass abundances with fragment size. Overall, fishes exhibited mostly linear relationships between abundance and fragment area, suggesting that kelp-associated fishes are more affected by habitat loss than by fragmentation. When incorporating kelp forests of larger area, however, formerly linear functions became non-linear, indicating that habitat fragmentation may become more important at larger spatial scales. At the scale of small kelp patches, the densities of *Paralabrax clathratus* and *Oxyjulis californica* were unrelated to patch size, and recruitment occurred in the smallest patches and was highly variable for both species. These results may provide resource managers with important information on the relative effects of habitat loss and fragmentation in the conservation and management of coastal fishes.

KEY WORDS: Disturbance · Habitat fragmentation · Patch size · Giant kelp · *Macrocystis pyrifera* · Reef fishes · Recruitment

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INTRODUCTION

A long-standing goal of ecology has been to understand the relationships between organisms and the habitats in which they reside (Bell et al. 1991). More recently, there has been a focus on the effects of habitat loss and fragmentation on biodiversity (Fahrig 2003) and the distribution and abundance of species (Wiegand et al. 2005). Relationships between an organism and the size of its habitat certainly vary among taxa (birds: Conner & Rudolph 1991; lizards: Hokit & Branch 2003; beetles: Crist & Ahern 1999).

However, studies that have investigated the effects of disturbance on habitats have focused primarily on the loss of habitat and not on fragmentation explicitly (but see Fahrig 2003 and Johnson & Heck 2006).

Habitat fragmentation has been described as a landscape process involving habitat loss, reduced patch size, and an increase in the distance among patches of remaining habitat as a result of both natural or anthropogenic disturbances (Andrén 1994). Such disturbances vary in magnitude and fragment habitat differentially, which, in turn, produces species-specific responses depending on an organism's ecological requirements. In

many studies, however, the effects of habitat loss have not been sufficiently decoupled from habitat fragmentation and are often examined at small spatial scales, both of which may result in equivocal interpretation of the results (Fahrig 2003).

Studies of fragmentation in marine environments are relatively few and for the most part have focused on seagrass habitats (Eggleston et al. 1998, Hovel & Lipcius 2001, 2002; but see Caley et al. 2001). These studies suggest that the density and survival of invertebrates vary with respect to patch size and habitat structural complexity. For example, shrimp are more abundant in small patches of seagrass because of the importance of a large perimeter-to-area ratio for feeding (Eggleston et al. 1998), whereas the survival of juvenile blue crabs is greater in more structurally complex habitat as a refuge from predation, regardless of patch size (Hovel & Lipcius 2002). The effects of patch size on local invertebrate communities also vary. Although a greater number of invertebrate taxa and differences in the composition of assemblages occur in larger versus smaller seagrass habitats (Bowden et al. 2001), the diversity of invertebrates may be affected more by the presence of seagrass than by its patch size (Hirst & Attrill 2008). In contrast to invertebrates, few studies have focused on the consequences of habitat fragmentation and patch size for marine fishes in seagrass ecosystems (Fernandez et al. 2005, Jelbart et al. 2006, Johnson & Heck 2006).

On temperate rocky reefs, considerable habitat is provided by macroalgae in the form of kelps (e.g. Dayton 1985, Foster & Schiel 1985). The density and abundance of many temperate reef fishes are positively related to the presence and abundance of kelps (Choat & Ayling 1987, Ebeling & Hixon 1991), particularly giant kelp *Macrocystis pyrifera* in California, USA (reviewed by Stephens et al. 2006), and elsewhere (Moreno & Jara 1984). Recruitment (input of young fish) of reef fishes in kelp habitats is strongly influenced by the structural complexity of kelps (Carr 1991, 1994, Anderson 1994) as a refuge from predation (Ebeling & Laur 1985, Anderson 2001, Johnson 2006). Both observational (Larson & DeMartini 1984, Bodkin 1986, DeMartini & Roberts 1990, Holbrook et al. 1990) and experimental (Bodkin 1988, Carr 1991, 1994, O'Connor & Anderson 2010) studies have shown that reductions in the density of giant kelp negatively affect the abundance of recruits and older reef fishes. Consequently, disturbances that result in the loss and fragmentation of kelp forests have the potential to cause substantial variation in recruitment and the abundance of rocky reef fishes.

Importantly, disturbances to giant kelp forests that result in the thinning, fragmentation, or absence of kelp are common. Winter storms can reduce the densities of giant kelp for several kilometers of coastline (Dayton et al. 1992), and more severe events such as the El Niño Southern Oscillation (ENSO) are capable of completely removing kelp at a much larger spatial scale (Edwards & Hernandez-Carmona 2005, Edwards & Estes 2006). Kelp grazing by sea urchins may lead to severe deforestation and fragmentation of nearshore kelp forests (Cowen et al. 1982, Ebeling et al. 1985, Springer et al. 2003). Anthropogenic disturbance such as sedimentation can reduce the density of kelp by decreasing the amount of light available for photosynthesis (Tegner et al. 1995) or covering young propagules, preventing their growth and development (Devinny & Volse 1978). Given the many disturbances capable of fragmenting kelp forests and the importance of kelp structural complexity to recruitment and the abundance of fishes, fragmentation may have adverse effects on reef fish populations.

In this study we investigated (1) the effects of fragmentation of giant kelp forests on the density and abundance of rocky reef fishes, and (2) the relationship between kelp patch size and recruitment of kelp-associated fishes at a smaller spatial scale. For the first objective, it is important to note whether and how the densities and extrapolated abundances of fishes may change across a gradient of kelp fragmentation to provide insight on the relative importance of habitat loss and fragmentation within kelp forests (Fig. 1). For example, a species that exhibits similar numerical or biomass densities across sizes of fragments should exhibit a simple positive linear relationship between fish abundance and fragment area, and because of this additive relationship, the amount and not the size of the habitat is most important, indicating that habitat loss has a much greater impact on kelp forest fishes than fragmentation. Alternatively, a species that increases in density with increasing fragment size should reveal a positive, exponential increase in the abundance of fishes because of the combination of increasing density and habitat area. In this case, habitat fragmentation should be more important than habitat loss because the abundance of fishes declines substantially with smaller differences in the degree of fragmentation. By contrast, if the density of fish is negatively related to fragment size, a positive but saturating asymptotic function in fish abundance would occur with increasing fragment size. Here, both habitat loss and fragmentation may vary in their influence on kelp forest fishes depending upon the amount of loss and the resulting distribution in size of fragments. Consequently, the frequency and strength of these relationships may have implications for the management of coastal fishes in rocky reef habitats.
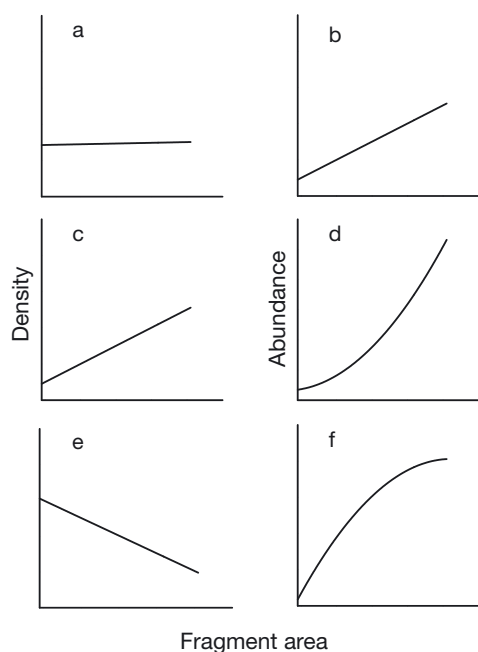
Fig. 1. Predicted relationships between the density and abundance of fishes as a result of habitat loss and fragmentation. (a,b) If density does not differ with fragment area, an additive relationship between abundance and fragment area is the result, indicating that habitat loss is more important than fragmentation. (c,d) If density increases with fragment area, an exponential relationship between abundance and fragment area is realized, indicating that habitat fragmentation is more important than loss. (e,f) If density decreases with fragment area, a saturating, asymptotic function between abundance and fragment area occurs, in which the relative importance of habitat fragmentation and loss depends upon the shape of the curve relative to fragment area

MATERIALS AND METHODS

Study system. This study was conducted on the leeward side of Santa Catalina Island, near the Wrigley Marine Science Center (33° 27' N, 118° 29' W). Rocky reefs along the coastline of the island generally slope steeply with depth, and forests of giant kelp occupy a relatively narrow but consistent width (~20 m) perpendicular to the shoreline. In addition, the topography of the islands reduces the distribution of other large understory stipitate kelp, which occur in highest abundance in very shallow depths. This configuration of kelp provided an exceptional opportunity to experimentally test the effects of habitat fragmentation in giant kelp forests, because the width of kelp forests, which may alter current flow and velocity (Jackson 1997) and thus the settlement and the distribution of fishes in our study area, is not confounded with fragment size. Three sites spanning a distance of 13 km were selected in which kelp forests were sufficient in length and similar in configuration for manipulations of habitat fragmentation to be performed (Fig. 2a).

Habitat fragmentation and fish abundance: a meso-scale experiment. *Experimental design:* In March and June 2005, a series of fragments of kelp forest (100, 200, 400, 600, 1000, and 1600 m^2) were created at each of the 3 study sites in a randomized block design (Fig. 2b). To establish treatments, meter tapes were laid for 300 m parallel to shore at the deepest edge of the kelp forest, and flagging tape was used to mark the placement of each fragment. The dimensions of each fragment, which correspond to the area of each treatment listed above were ~20 m wide and 5, 10, 20, 30, 50, and 80 m long, respectively. To maintain discrete treatments and reduce the potential movement of post-settlement recruit fishes among fragments, a distance of 15 m between adjacent fragments was cleared of all giant kelp and understory stipitate kelps from the outer to the inner edge of the kelp forest (Fig. 2b). Thus, habitat loss between fragments and among sites was held constant to explicitly examine the effects of habitat fragmentation on kelp forest fishes. Giant kelp was removed by severing individuals just above the holdfast and before the primary dichotomy of stipe bifurcation. All kelps that appeared in clearings between fragments after the initial clearing in 2005 were removed before surveys of fishes were initiated in 2006.

To ensure that the effects of fragmentation were not confounded by differences in the density of giant kelp, estimates of density were determined along transects within fragments at each site for each year in which habitat fragmentation was studied (2005 and 2006). Within each fragment, 2 to 6 random transects (2 m width × 20 m length, or 40 m^2) were surveyed to determine the density of adult kelp (individuals with at least 4 fronds and >1 m in height); 2 and 6 transects were established in the 100 m^2 and 1600 m^2 fragments respectively, and 4 transects were surveyed in all other fragments (Table 1a). A different number of transects was used for each fragment at a given site to obtain more precise estimates of kelp density (Table 1b). For statistical analyses, all densities obtained from belt transects were averaged into a single data point per fragment (see analyses section). All transects were surveyed perpendicular to shore from the outer to the inner edge of each kelp fragment.

This experiment was planned for 3 yr, but 2 sites were compromised in 2007 due to a natural cliff collapse and underwater rock slide in the nearshore environment at Arrow Point and Empire Landing, respectively. Therefore, we investigated whether relationships between the density and abundance of fishes and the area of larger kelp forests were consistent with the results from experimental habitat fragmentation. We conducted single surveys of recruit and older fishes in August 2007 at the remaining intact experimental site (Quarry, surveyed in the same manner as in 2005 and 2006) and at
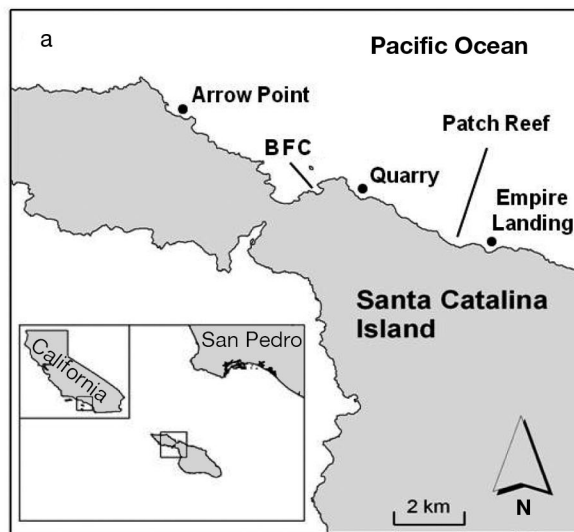
Fig. 2. (a) Study sites at Santa Catalina Island, California. Three sites were used for meso-scale experimental habitat fragmentation in kelp forests: Arrow Point, Quarry, and Empire Landing. Two sites were used for the small-scale patch size experiment: Big Fishermen Cove (BFC) and Patch Reef. (b) Experimental design of habitat fragmentation at each of 3 sites at Santa Catalina Island in 2005. Kelp was cleared in 15 m sections to create kelp forest fragments of ~20 m width by 5, 10, 20, 30, 50, and 80 m length alongshore, representing areas from 100 m² to 1600 m²
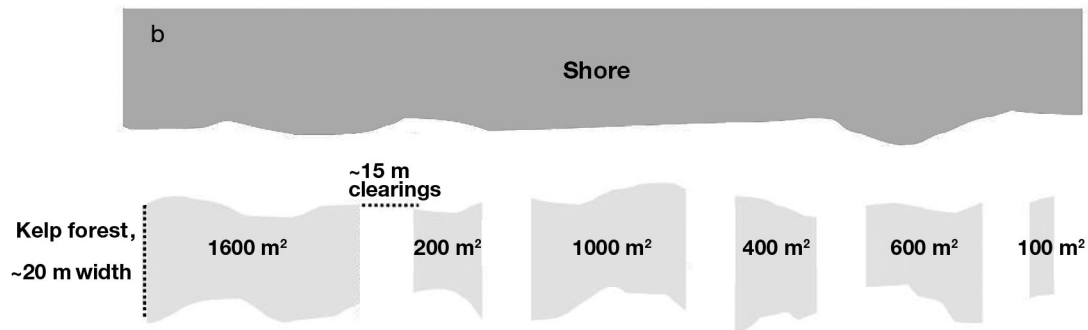
Table 1. (a) Belt transect surveys conducted in meso-scale experiments to assess the effects of habitat fragmentation and loss on kelp forest fishes in 2005 to 2006. (b) Number of replicates and patches used for each treatment in both meso- and small-scale experiments, respectively

(a)

Survey type	Dimensions	Area or volume	Depth strata surveyed
Kelp	2 m (w) × 20 m (l)	40 m²	Bottom
Recruit fishes	1 m (w) × 1 m (h) × 20 m (l)	20 m³	Canopy, midwater, bottom
Older fishes	2 m (w) × 2 m (h) × 20 m (l)	80 m³	Midwater, bottom

(b)

	Meso-scale experiment		Small-scale experiment		
Fragment area (m²)	No. transects	No. replicates	No. individual kelp/ patch area (m²)	No. patches 2006	No. patches 2007
100	2	3	1/0.06	4	3
200	4	3	2/0.25	4	3
400	4	3	3/0.43	4	3
600	4	3	4/1.0	3	2
1000	4	3	6/1.7	3	2
1600	6	3	9/4.0	1	1
2580*	8	1	12/6.0	1	0
4250*	10	1	16/9	1	0
4540*	12	1			

*observational surveys of naturally occurring kelp forests in 2007

3 naturally occurring kelp forests that were similar in configuration to the manipulated forests used to explore habitat fragmentation. The areas of the natural kelp forests surveyed were 2580 m^2, 4250 m^2, and 4540 m^2, measured by extending a transect tape parallel to shore from the beginning to the end of the forest and multiplying the value obtained by the average width of the kelp forest (20 m). Surveys of fishes were conducted by establishing 8 to 12 transects (depending on the size of the kelp forest) of the same orientation and dimensions used in surveys of older life stage and recruit fishes (see below) in the experiment on habitat fragmentation (Table 1b).

Surveys of recruit and older fishes: Within each fragment, belt transects were surveyed for recruit fishes (young fish which recently settled from the water column to kelp, up to 4 mo old and ~2 to 8 cm total length, TL) and for older life stages (juvenile and adult fishes). Two to 6 randomly positioned transects were used per fragment, depending upon fragment area (see 'Experimental design'). More transects were established in larger fragments to obtain more precise estimates of fish density within our largest fragments. Conversely, fewer transects were used in smaller fragments because there was less habitat to survey and only 2 transects fit within the area of the smallest fragments (Table 1b). Transects were followed from the deeper outer edge of the kelp forest (maximum of 15 m depth) perpendicular to and toward the shore to survey the densities of fishes across depths. Surveys of recruit fishes were conducted in July, August, and October 2005, in June, July, and August 2006, and in 2007 at Quarry. To quantify recruit fishes at each transect position, we sampled fishes in 3 depth strata: kelp canopy (0–2.5 m depth), midwater (midway between the canopy and seafloor; 2.5–7.5 m depth), and bottom (7.5–15 m depth). We used 1 m wide × 1 m high × ~20 m long (20 m^3) transects, with transect length depending on the estimated width of the kelp fragment on a transect. An observer would first swim slowly in the kelp canopy towards and perpendicular to shore, recording all species and sizes (TL, cm) of recruits. Upon reaching the inner edge of the kelp forest, the observer would descend to midwater and swim offshore while again recording the species and sizes of recruits, maintaining a depth approximately equidistant between the water surface and seafloor. Once the outer perimeter of the kelp forest was again reached, the diver would descend once more and record recruits along the bottom while deploying a meter tape to measure the distance traversed to the inner edge of the kelp forest. This distance was then used to determine the mean number of recruit fishes per unit volume (~20 m^3) per stratum for each transect.

For surveys of older life stages of fishes, juvenile (~1 yr or older) and adult fishes were combined into 1 category (hereafter referred to as older fishes) because our observations and prior studies did not reveal substantive differences in habitat use between these 2 life stages (e.g. Larson & DeMartini 1984). Surveys to explore the effects of fragmentation on older fishes were performed in July and August 2005 and 2006, and July and August 2007 at Quarry. The dimensions of transects for these surveys were 2 m high × 2 m wide × ~20 m long (80 m^3) to encompass the large size and mobility of older fishes, and fishes were enumerated by species with visual estimates of their size (TL, cm). No transects were established in the kelp canopy because older fishes are not as strongly associated with this stratum as are young recruits (e.g. Anderson 1994).

Kelp patch size and recruitment: experimental design. To determine the relationship between recruitment of kelp-associated fishes and patches of kelp at smaller spatial scales, we experimentally manipulated kelp in isolated stands. In July 2006, individual kelp were translocated from Patch Reef (Fig. 1a) to a featureless sand bottom adjacent to the reef and secured with rope and earth anchors. Patches of kelp were constructed with increasing area but standardized to the density of kelp (individuals spaced equally from one another at a distance of 1 m and treatments were separated from one another by a distance of 10 m in order to prevent the movement of post-settlement recruit fishes). Each patch received 1, 2, 3, 4, 6, 9, 12, or 16 individual kelp, constituting total patch areas of 0.06, 0.25, 0.43, 1.0, 1.7, 4.0, 6.0, and 9.0 m^2, respectively. We established 4 plots for each patch area of 0.06, 0.25, and 0.43 m^2, 3 plots for patch areas of 1.0 and 1.7 m^2, and 1 plot for patch areas of 4.0, 6.0, and 9.0 m^2 (Table 1b). A greater number of smaller patches were constructed because of expected higher variability in recruitment with decreasing patch size.

After construction of patches, recruitment of fishes was monitored after 2 and 4 wk. Teams of 2 (smaller patches) or 4 observers (large patches ≥6 individual kelp) counted recruits to reduce potential double-counting and to ensure that all recruits were included. Within each patch, each individual kelp was searched intensively for all recruits associated with giant kelp, beginning at the kelp canopy and descending to the substratum. On larger patches, censuses from each observer were summed to obtain an overall abundance of recruits in each patch.

This same experiment was repeated in June 2007 at a different site (Big Fisherman Cove, Fig. 2a). Three plots each were constructed for patch areas of 0.06, 0.25, and 0.43 m^2, 2 for areas of 1.0 and 1.7 m^2, and 1 for a patch area of 4.0 m^2. We did not construct plots >4.0 m^2 because of limited space on sandy bottom and a focus on smaller patch areas because of variability in recruitment observed in small patches the previous year. All plots ≥0.43 m^2 in patch area were censused by

multiple observers to reduce the probability of double-counting, and recruitment was monitored after 2, 4 and 6 wk.

Analyses. *Habitat fragmentation:* For a given survey at a site within a year, the numerical densities of both recruit and older fishes per fragment were calculated by summing counts of fishes on a transect across depth strata and standardizing the density per unit volume (100 m^3). The densities obtained for each transect were then averaged to obtain a mean density of fish per fragment. The mean densities for each fragment at a site were then averaged across monthly surveys to determine an overall mean density for each fragment size and year. The overall mean densities for each year (2005, 2006) were then averaged to obtain the mean density of fish for each fragment at a site observed over the course of the experiment. The same procedure was used to determine biomass density; standard length measurements of older fishes were converted to weight using length–weight relationships (Cailliet et al. 2000, T. Anderson unpublished data), from which biomass density per unit volume was determined.

We focused on abundance with respect to habitat fragmentation because the densities of fishes determined in the 3 strata (kelp canopy, midwater, bottom) were integrated across the water column. To obtain the numerical and biomass abundances of fishes, numerical and biomass densities were extrapolated by integrating the density of fishes (ind. 100 m^{-3}) in each depth stratum proportionally to the extent of the water column to determine the density per unit area of reef (ind. 100 m^{-2}), taking into account the larger volume represented by midwater transects. This area was then extrapolated to the size of a kelp fragment to achieve an overall abundance. The numerical and biomass abundances of fishes per fragment among sites were then compared to fragment size using linear and non-linear regression.

The relationship between the abundance of fishes and kelp fragment size was described by the model (linear, exponential, or asymptotic) with the best fit as determined by the highest coefficient of determination (r^2). The 3 models were also compared using Akaike's Information Criterion (AIC; Motulsky & Christopoulos 2003). For all species of recruit and older fishes that exhibited significant non-linear relationships between their numerical or biomass abundance and fragment size, linear regression as a conservative standard of habitat loss was also performed for comparison with the fit of non-linear models. The abundances of recruit and older fishes from single surveys at Quarry and 3 larger naturally occurring kelp forests in 2007 were summarized using the same methods as described above and analyzed using linear and non-linear regression.

Statistical analyses were conducted only for those species with sufficient densities for meaningful com-

parisons, although analyses of all species combined contained all fishes surveyed (Table 2). Older fishes included for analysis by species, in order of decreasing density, were *Chromis punctipinnis*, *Paralabrax clathratus*, *Brachyistius frenatus*, *Hypsypops rubicundus*, *Girella nigricans*, *Halichoeres semicinctus*, *Semicossyphus pulcher*, and *Oxyjulis californica*. Recruit fishes included for analysis were *C. punctipinnis*, *P. clathratus*, *B. frenatus*, and *O. californica*.

To determine differences in the density of kelp among sizes of fragments and sites, counts of kelp fronds among transects in a fragment were averaged to assess the density of fronds (no. 40 m^{-2}) per fragment at each site. The densities of kelp fronds were then averaged between years (2005, 2006) and a 1-way blocked analysis of variance (ANOVA) was used to determine whether the mean density of fronds differed significantly among fragments and sites. Data were inspected for assumptions of normality and homogeneity of variances and log-transformed as necessary to meet these assumptions.

Patch size and recruitment: In the first experiment to examine kelp patch size and recruitment of fishes, only

Table 2. Fish species (older juveniles/adults and recruits) recorded during kelp forest surveys (2005 to 2007), in decreasing order of abundance; *sufficiently abundant for statistical analysis. All species recorded were incorporated into analyses of 'all species combined'

Species	Common name
Older juvenile and adult fishes	
Chromis punctipinnis	Blacksmith*
Paralabrax clathratus	Kelp bass*
Brachyistius frenatus	Kelp perch*
Hypsypops rubicundus	Garibaldi*
Girella nigricans	Opaleye*
Halichoeres semicinctus	Rock wrasse*
Semicossyphus pulcher	California sheephead*
Oxyjulis californica	Señorita *
Medialuna californiensis	Halfmoon
Embiotoca jacksoni	Black perch
Xenistius californiensis	Salema
Heterostichus rostratus	Giant kelpfish
Rhacochilus toxotes	Rubberlip seaperch
Hermosilla azurea	Zebraperch
Anisotremus davidsonii	Sargo
Paralabrax nebulifer	Barred sand bass
Rhacochilus vacca	Pile perch
Hypsurus caryi	Rainbow seaperch
Recruit fishes	
Chromis punctipinnis	Blacksmith*
Paralabrax clathratus	Kelp bass*
Brachyistius frenatus	Kelp perch*
Oxyjulis californica	Señorita*
Heterostichus rotratus	Giant kelpfish
Embiotoca jacksoni	Black perch
Halichoeres semicinctus	Rock wrasse
Cymatogaster aggregata	Shiner perch

the second survey (1 mo) was employed because no recruits were observed during the first survey at 2 wk. For the second experiment, observations of recruits were averaged over 3 biweekly surveys. For both experiments, the relationship between patch size and the density of recruits was examined with linear regression and a negative exponential regression function. Linear regression was performed on log-transformed data to meet the assumption of homogeneity of variances.

RESULTS

Effects of habitat fragmentation on kelp forest fishes

Because kelp density did not differ among sites or fragments throughout our experiment (p = 0.82 and 0.20 for fragment and site, respectively) we examined the observed relationships between fish numerical or biomass abundance and fragment size. The relationships between the numerical abundance of older fishes and kelp fragment size were described by different positive regression functions among species (Table 3). We selected the best fit models using the highest coefficient of determination (r^2). Model selection using AIC evidence ratios did not provide clear evidence with our data to favor any one model over another for all species and life stages (see Tables 3 & 4).

For all species combined, there was a positive linear function between numerical abundance and fragment size (Fig. 3a). Of 3 common kelp forest fishes in southern California, *Chromis punctipinnis* exhibited a linear function with numerical abundance (Fig. 3c), while *Oxyjulis californica* and *Paralabrax clathratus* were best described by exponential (Fig. 3e) and asymptotic (Fig. 3g) functions, respectively. The biomass abundance of older fishes (Table 3) revealed positive linear relationships with fragment size for all species combined (Fig. 3b) and all species analyzed independently, except for *O. californica* (Fig. 3f) and *Halichoeres semicinctus*, which exhibited exponential and asymptotic relationships, respectively. For recruit fishes (Table 3), numerical abundance was linearly related to kelp fragment size for all species combined, *C. punctipinnis*, and *O. californica* (Fig. 4a–c). *P. clathratus* (Fig. 4d) and *Brachyistius frenatus* were best described by asymptotic relationships.

Interestingly, the numerical abundances of fishes in 2007 at Quarry (the only remaining intact site) and 3 much larger natural kelp forests revealed relationships

Table 3. Relationships between numerical or biomass abundance and kelp fragment size for older fishes and recruits in 2005 and 2006 combined. Best-fit relationships between abundance of fishes and kelp fragment size as determined by the highest r^2 values. 'Percentage more variation' is the amount of additional variation explained by the non-linear model than by a linear model. The Akaike Information Criterion (AIC) evidence ratio is a multiplier indicating the 'better' fit of a linear model vs. the non-linear models. 'All species combined' includes all older fishes and recruit fishes recorded on surveys (see Table 2). Full species names are listed in Table 2

	Species	Numerical or biomass abundance		Regression function	% more variation	AIC evidence ratio
		r^2	p			
Older fishes	All species combined	0.95	<0.001	Linear	–	1.15
Numerical	*C. punctipinnis*	0.79	<0.001	Linear	–	1.11
abundance	*P. clathratus*	0.87	<0.001	Asymptotic	4	1.12
	B. frenatus	0.76	<0.001	Exponential	1	1.27
	H. rubicundus	0.87	<0.001	Linear	–	1.11
	G. nigricans	0.68	<0.001	Asymptotic	16	1.12
	H. semicinctus	0.84	<0.001	Asymptotic	7	1.11
	S. pulcher	0.73	<0.001	Exponential	6	1.30
	O. californica	0.66	0.002	Exponential	13	1.24
Biomass	All species combined	0.85	<0.001	Linear	–	1.11
abundance	*C. punctipinnis*	0.62	0.002	Linear	–	1.11
	P. clathratus	0.89	<0.001	Linear	–	1.20
	B. frenatus	0.87	0.001	Linear	–	1.11
	H. rubicundus	0.90	<0.001	Linear	–	1.49
	G. nigricans	0.41	0.005	Linear	–	1.26
	H. semicinctus	0.85	<0.001	Asymptotic	2	7.50
	S. pulcher	0.61	<0.002	Linear	–	1.16
	O. californica	0.69	0.003	Exponential	11	1.25
Recruit fishes	All species combined	0.84	<0.001	Linear	–	1.12
Numerical	*C. punctipinnis*	0.42	0.03	Linear	–	1.11
abundance	*P. clathratus*	0.52	0.007	Asymptotic	8	1.26
	B. frenatus	0.45	<0.002	Asymptotic	14	1.43
	O. californica	0.42	0.03	Linear	–	1.22

(Table 4) that often differed from those observed at our experimental sites in 2005/2006 (Table 3). For example, the numerical abundances of all species combined, *Chromis punctipinnis*, and *Hypsypops rubicundus* in 2007 showed exponential, linear, and asymptotic

relationships with the size of kelp fragments and forests (Fig. 5a–c). By contrast, these species exhibited either linear or asymptotic functions of these relationships in 2005/2006. Including larger naturally occurring kelp fragments in our analyses also changed the relationships between the biomass abundance of older fishes and the size of kelp fragments and forests. The biomass abundances of fishes observed in 2005/2006 were altered from mostly additive functions to either asymptotic or exponential relationships (Table 4). For recruit fishes, the numerical abundances of recruits surveyed in 2007 (Table 4) also revealed relationships that differed from those obtained in 2005/2006. The numerical abundances of all species combined and *Oxyjulis californica* were exponentially related to the size of kelp fragments and forests in 2007, but both showed linear relationships in abundance with fragment size in 2005/2006. *C. punctipinnis* showed additive relationships for both time periods. *Paralabrax clathratus* was not included in these analyses because recruitment was negligible in 2007.
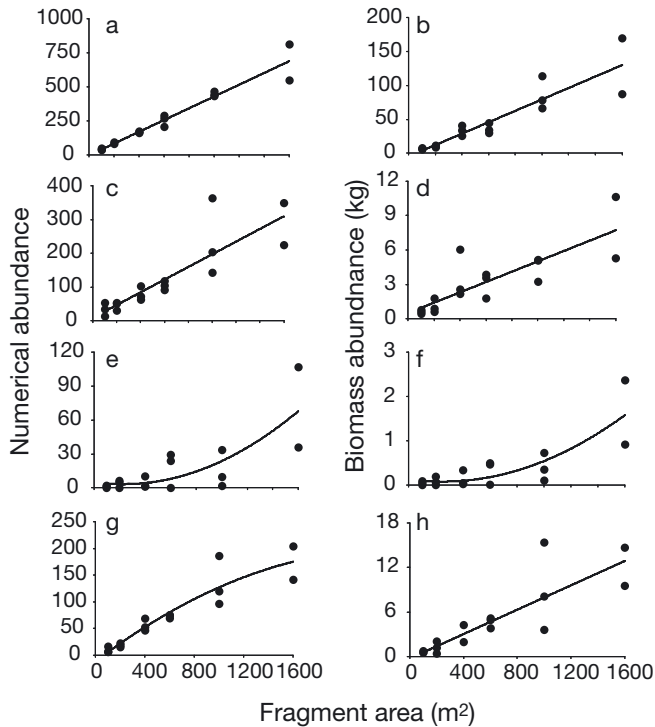

Fig. 3. Relationships between the numerical (left column) and biomass (right column) abundance of older fishes and fragment size for (a,b) all species combined, (c,d) *Chromis punctipinnis*, (e,f) *Oxyjulis californica*, and (g,h) *Paralabrax clathratus* in 2005 to 2006
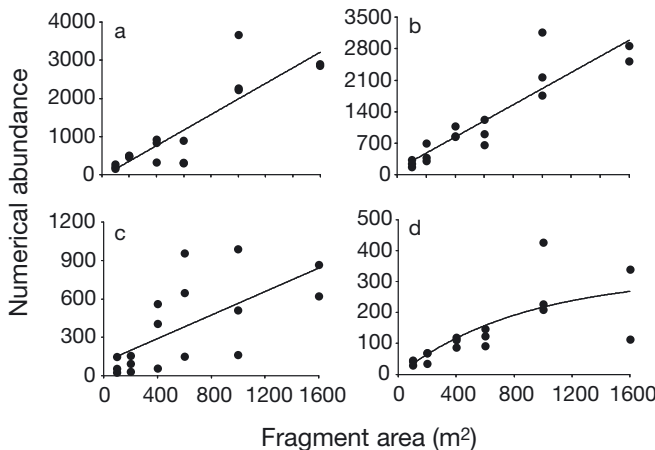

Fig. 4. Relationships between the numerical abundance of recruit fishes and fragment size for (a) all species combined, (b) *Chromis punctipinnis*, (c) *Oxyjulis californica*, and (d) *Paralabrax clathratus* in 2005 to 2006
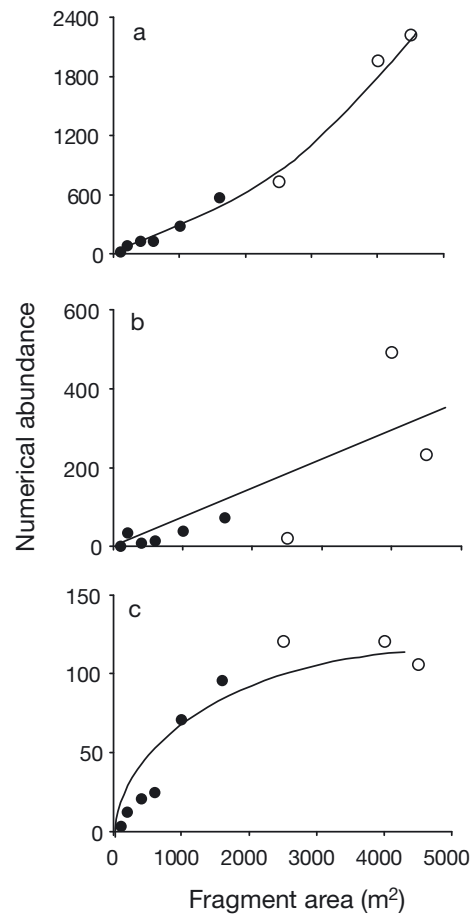

Fig. 5. Relationship between the numerical abundance of older fishes and kelp fragment or forest size for (a) all species combined, (b) *Chromis punctipinnis*, and (c) *Hypsypops rubicundus* in 2007. (●) data from experimental fragments at Quarry; (○) data from naturally occurring kelp forests

Table 4. Relationships between numerical or biomass abundance and kelp fragment/forest size for recruits and older fishes in 2007. Regression functions describe the best-fit relationships as determined by r^2 values. The meso-scale regression function shows the best-fit models from the meso-scale experiment in 2005 and 2006 combined. The Akaike Information Criterion (AIC) evidence ratio is a multiplier indicating the 'better' fit of a linear model vs. the non-linear models. 'All species combined' includes all older fishes or recruit fishes recorded on surveys (see Table 2). Full species names are listed in Table 2

| | Species | Numerical or biomass abundance | | Regression function | Meso-scale regression | AIC evidence ratio |
		r^2	p			
Older fishes	All species combined	0.96	<0.001	Exponential	Linear	1.12
Numerical	P. clathratus	0.95	<0.001	Exponential	Asymptotic	1.13
abundance	H. semicinctus	0.96	<0.001	Exponential	Asymptotic	1.14
	C. punctipinnis	0.66	0.01	Linear	Linear	1.12
	H. rubicundus	0.94	<0.001	Asymptotic	Linear	1.11
	B. frenatus	0.71	0.004	Linear	Linear	1.13
Biomass	All species combined	0.96	0.05	Asymptotic	Linear	1.12
abundance	P. clathratus	0.94	0.002	Exponential	Linear	1.11
	H. semicinctus	0.98	<0.001	Exponential	Asymptotic	1.13
	C. punctipinnis	0.63	<0.001	Exponential	Linear	1.14
	H. rubicundus	0.90	<0.001	Asymptotic	Linear	1.16
	B. frenatus	0.74	0.02	Asymptotic	Linear	1.11
Recruit fishes	All species combined	0.91	0.008	Exponential	Linear	1.40
Numerical	C. punctipinnis	0.50	0.02	Linear	Linear	1.17
abundance	O. californica	0.97	<0.001	Exponential	Linear	1.11

Relationships between kelp patch size and recruitment

In 2006, *Paralabrax clathratus* was the only species with substantial recruitment to the experimental array, whereas in 2007, recruits consisted mostly of *Oxyjulis californica*. The density of recruit *P. clathratus* was unrelated to kelp patch size (p = 0.33) in 2006. Both high densities of recruits and high variability in recruitment (Fig. 6a) were observed for smaller patches ≤2 m^2. Similar to *P. clathratus* recruitment in 2006, the density of *O. californica* in 2007 was unrelated to kelp patch size (p = 0.51), and recruitment was high and variable at smaller patch sizes (Fig. 6b).

DISCUSSION

Understanding habitat fragmentation and its effects on marine organisms is becoming increasingly important due to the frequency, magnitude, and sometimes permanency of the many natural and anthropogenic sources of disturbance. Relative to terrestrial ecosystems, however, few studies have been conducted on habitat fragmentation in the marine environment. Of these, seagrass beds have been a primary focus, with the effects of fragmentation examined observationally at larger spatial scales (Hovel & Lipcius 2002) or experimentally through manipulation of habitat or organisms at much smaller spatial scales (Eggleston et al. 1998, Healey & Hovel 2004). Few studies have attempted to decouple the effects of habitat loss from

fragmentation (but see Caley et al. 2001), making the results difficult to interpret (Fahrig 2003).

In our study of habitat fragmentation and its effects on the recruitment and abundance of kelp forest
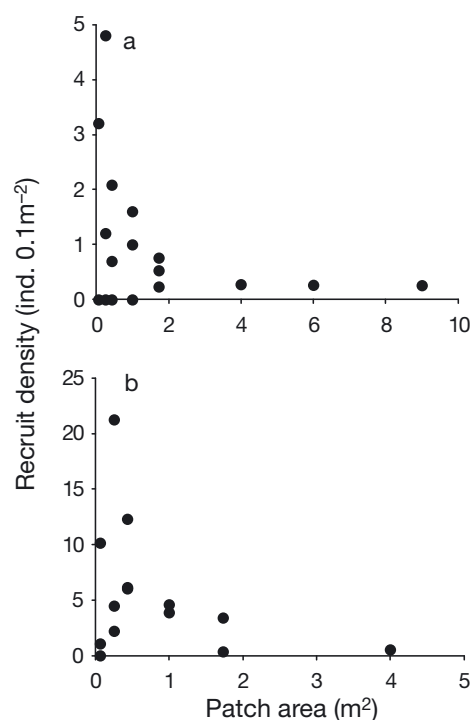

Fig. 6. *Paralabrax clathratus* and *Oxyjulis californica.* Relationship between the density of recruit fishes and kelp patch size for (a) *P. clathratus* in 2006 and (b) *O. californica* in 2007

fishes, we used meso-scale (100s of meters) experimental manipulations to investigate whether habitat fragmentation influences the density and abundance of recruit and older fishes within and among giant kelp forests. Our approach was to specifically evaluate the relative importance of habitat fragmentation versus habitat loss by determining the shape of the regression functions in the numerical and biomass abundances of fishes across a gradient of kelp fragment size. We selected the best fit models using the highest coefficient of determination (r^2) because comparisons made using AIC did not improve our ability to select the best model. Overall, we often observed linear relationships between the numerical or biomass abundance and kelp fragment size for many species, and for those functions that were non-linear, there was little added variation explained in comparison to a linear model.

The additive, linear functions exhibited in many species and in all instances for all species combined for numerical abundance and biomass and across life stages suggest that kelp forest fishes are much more strongly affected by the loss of habitat than by its fragmentation, consistent with some studies in other marine (Caley et al. 2001) and terrestrial ecosystems (Fahrig 2003). The prevalence of linear functions observed here is likely a consequence of similar but variable densities of fishes across a gradient in kelp fragment size. In this temperate marine ecosystem, the mobility of many older juvenile and adult fishes (Lowe & Bray 2006), and the high potential for dispersal of pre-settlement larvae (Caley et al. 1996, Carr & Syms 2006) may render habitat fragmentation inconsequential in affecting the density of most recruit or older fishes within and among kelp forests at this spatial scale. The habitat associations of recruit fishes in particular occur at small spatial scales and are largely influenced by structural habitat complexity and are likely to be much less affected by the areal extent of the habitat itself. One consequence of habitat fragmentation that we did not address is the distance between or isolation of fragments. Because of the much greater mobility and dispersal potential of these fishes, however, we do not expect the degree of isolation to be important relative to habitat fragmentation area and loss in kelp forests. Many older fishes are highly mobile and are more loosely associated with their habitat and therefore may travel among fragments of kelp forests with little consequence. Similarly, recruits of kelp-associated fishes are capable of settling from the plankton to patches of kelp regardless of their isolation from one another.

Despite the experimental fragmentation of kelp forests, incorporating even larger natural kelp forests suggests that larger areas of discrete kelp forests, separated by less suitable habitat, may be an important issue in describing the relationship between fish abundance and habitat area. When including much larger kelp forests in surveys of the density and abundance of fishes in 2007, the relationships between numerical abundance or total biomass and kelp fragment size were altered from linear to non-linear functions for several species and for all species combined. Recruit fishes also exhibited similar changes, exhibiting exponential functions for all species combined and for *Oxyjulis californica* that were described by linear functions from the meso-scale experiment. Although the greater amount of variation explained by these non-linear functions was generally <15% versus a linear model, non-linear relationships were observed with a much greater frequency. As kelp forests become much larger and are defined by discrete boundaries of rocky reef habitat, fishes may be more likely to restrict their movements within kelp habitat at the scale of these kelp forests. These results must be interpreted with caution, however, because we were able to survey only 3 large kelp forests, and the data from 2 of these forests were important drivers of the non-linear relationships.

By contrast, the sizes of very small patches of giant kelp appear to be unrelated to recruitment of kelp-associated fishes. Both *Paralabrax clathratus* and *Oxyjulis californica* certainly are capable of settling to small patches of habitat consisting of an individual kelp. Although there is high variation in recruitment among smaller patches, the density of recruits does not increase with patch area. Variation in recruitment of kelp-associated fishes appears to be much more strongly linked to structural habitat complexity in the density of fronds or individuals (Ebeling & Laur 1985, Carr 1994), blade biomass (Carr 1994), and the percentage cover of the kelp canopy (Anderson 1994). However, these results do not address the persistence of recruits in patches of different size. For example, if predator-induced mortality (Anderson 2001, Johnson 2006) is relatively higher in small than large patches because there is less physical refuge, the frequency distribution of sizes of kelp patches may be important in determining the magnitude of recruitment at a location. If so, fragmentation at small spatial scales may alter recruitment success more than these results suggest. Nonetheless, habitat loss appears to play a much larger role in recruitment success with kelp patch size than does the degree of fragmentation of kelp forests.

In summary, the patterns of density and abundance observed in this study are somewhat similar to previous research that describes the effects of habitat fragmentation in marine and terrestrial ecosystems. The effects of fragmentation can vary in strength and affect species differentially (Eggleston et al. 1998) and are

also dependent on the scale at which studies are conducted (Fahrig 2003). In this case, however, habitat loss is more likely to impact kelp forest fishes within kelp forests than fragmentation is, although fragmentation may assume a greater role in its effects among kelp forests at larger spatial scales.

The relationships described here may provide useful information to resource managers responsible for the conservation of nearshore habitats. The effectiveness of a marine protected area (MPA) is often assumed to be a reflection of its size because of the possibility of preserving a continuous stretch of productive marine habitat and its associated fauna (Claudet et al. 2008). This type of reserve strategy, however, may be more effective for sedentary species or species with low dispersal distances (such as surfperches, family Embiotocidae) and less appropriate for retaining species that are more mobile and have greater larval dispersal (Botsford et al. 2001, Kaplan et al. 2006). Recent modeling studies have suggested that the percentage of coastline incorporated into a reserve and the connectivity among reserves is a more critical component for MPA effectiveness than reserve size alone (Kaplan et al. 2006, Moffitt et al. 2009). Our results suggest that the densities of kelp forest fishes are more closely related to the presence of habitat than to habitat area. However, when considering the observational results we obtained when surveying well-defined large kelp forests, it is possible that fish–habitat relationships have the potential to change depending on spatial scale. In our study, data from large kelp forests defined by suitable rocky habitat suggests that the loss of kelp habitat may be increasingly important. A plausible mechanism for the higher abundances of fishes in these forests is that individuals may spend much more time over rocky reef habitat as opposed to moving over considerable distances of featureless sand bottom to other suitable habitat.

When implementing marine protected areas as a management tool (Greenville & Macaulay 2007, Claudet et al. 2008) to replenish coastal reef-associated fish populations in temperate regions, we suggest that one should consider the area of hard substratum (and thus kelp habitat) more so than its configuration (e.g. the fraction of rocky reef coastline within a proposed MPA), the prevalence and variability in the cover of kelp from disturbance as it relates to habitat loss and not fragmentation, and the distribution of larger kelp forests and the distances of unsuitable habitat between them with the goal of increasing residence times of economically important species within MPAs. Clearly, future research should address the causes and consequences of habitat loss and fragmentation of coastal marine habitats at scales appropriate for ecosystem-based management.

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