



# Consequences of habitat disturbance and recovery to recruitment and the abundance of kelp forest fishes

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## ARTICLE INFO

### Article history:

Received 6 October 2008

Received in revised form 14 December 2009

Accepted 27 January 2010

### Keywords:

Disturbance

Kelp forest

*Macrocystis pyrifera*

Recovery

Recruitment

Reef fishes

## ABSTRACT

The complete or partial removal of kelp forests due to disturbance can alter species composition and cause large reductions in the abundance of fishes in temperate zones. The effects of a gradient in disturbance that results in the thinning of kelp, however, have not been explored. We conducted manipulations corresponding to 0%, 33%, 66%, and 100% removal of *Macrocystis pyrifera* (L.) C. Ag at three sites along Santa Catalina Island, California. Surveys of fishes conducted 1–3 months after the removal of *M. pyrifera* revealed differences in recruitment for *Brachyistius frenatus* (Gill). Additionally, a trend was seen for *Oxyjulis californica* (Günther) showing an increase in recruit fish densities in treatments with higher amounts of *M. pyrifera*. For older life stages, there also were differences among treatments in the numerical densities of *Chromis punctipinnis* (Cooper), *Paralabrax clathratus* (Girard), and *B. frenatus* and in the biomass densities of *P. clathratus* and *B. frenatus*. Algae surveys conducted annually in the 2 years following disturbance showed the stipe densities of *M. pyrifera* among all treatments were at least as high as at the initiation of the experiment, indicating that treatments of *M. pyrifera* removal had recovered quickly to pre-disturbance levels. With one exception, there were no differences in recruitment or in the numerical or biomass densities of older juvenile and adult fishes among treatments in either of the two years following the initial disturbance. *M. pyrifera* in mature vs. recovering forests differs in its distribution and morphology, which might influence recruitment of kelp-associated fishes. To investigate these differences we conducted an experiment manipulating the distribution of adult and juvenile fronds of *M. pyrifera*. Recruitment of fishes was significantly higher on adult *M. pyrifera* and bundled fronds of juvenile *M. pyrifera* than on a dispersed distribution of juvenile *M. pyrifera*, indicating that the distribution of fronds primarily influences recruitment of kelp-associated fishes. Our results indicate that a gradient in disturbance and variation in the density of fronds of *M. pyrifera* influences recruitment and the distribution of older life stages of fishes, revealing some patterns at intermediate levels of removal that would not be observed by the simple presence or absence of this habitat. Although recovery of *M. pyrifera* to pre-manipulation levels was achieved over a relatively short period time in this study, variation in recruitment and the abundance of kelp forest fishes as a result of disturbance will depend on the intensity of the disturbance, the conditions that promote or delay habitat recovery, and the life history characteristics of individual species.

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## 1. Introduction

Disturbance plays a prominent role in ecosystems, having differential effects depending on its frequency and magnitude (Connell, 1978; Graham et al., 1997; Syms and Jones, 2000). For example, fire sweeping through a boreal forest or chaparral shrubland can have significant effects on tree distribution and species composition, depending upon the depth and intensity of the burn and post-fire competition and predation (Schimmel and Granstrom, 1996; Tyler, 1996). Similarly, extreme storms may have long-term consequences to rocky reef

communities by the removal of kelp forests (Dayton and Tegner, 1984; Ebeling et al., 1985). Subsequent recovery following disturbance often depends on the severity of the disturbance, and in certain situations, recovery may not reach a pre-disturbed state (Carpenter et al., 2001; Carr et al., 2003).

Sources of disturbance that result in the reduction and thinning of kelp forests can occur at widely different spatial and temporal scales (Edwards, 2004). In particular, local disturbances that can remove and thin kelp forests include strong storms (Dayton et al., 1984; Edwards and Hernandez-Carmona, 2005) and herbivory by urchins (Ebeling et al., 1985; Dayton et al., 1992). In addition to these natural sources of disturbance, anthropogenically caused disturbances such as gas-production effluent (Reed and Lewis, 1994), sedimentation from landslides (Konar and Roberts, 1996), and power generation (Schroeter et al., 1993) also have localized effects.

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Like terrestrial forests that often depend on a local seed bank for recovery from fire (Keeley, 1987; Enright and Lamont, 1989; Pierce and Cowling, 1991), recovery from disturbance of kelp forests in marine coastal environments may rely on both a seed bank of microscopic gametophytes (Carney and Edwards, 2006) and short- and long-range dispersal of propagules (Dayton et al., 1992; Reed et al., 1997, 2004). However, kelp forests may recover over a much shorter period of time following disturbance (Reed et al., 1988) due to much higher growth rates and shorter generation times. Full recovery of a *Macrocystis pyrifera* (L.) C. Ag. forest in central California can occur within 3 months under appropriate environmental conditions, although the recovery rate depends on the severity of the disturbance and the level of exposure of the forest (Graham et al., 1997). At its southern limit in Baja California, recovery of *M. pyrifera* can take decades due to increased mortality and recruitment failure, limited substratum availability, and competition with other algae (Edwards and Hernandez-Carmona, 2005).

*M. pyrifera* forests constitute an important habitat for rocky reef fishes in central and southern California (reviewed by Stephens et al., 2006). The structural habitat complexity and density of *M. pyrifera* influences the recruitment (Anderson, 1994; Carr, 1994a; Carr and Syms, 2006), density (DeMartini and Roberts, 1990), and assemblage structure (reviewed by Ebeling and Hixon, 1991) of kelp-associated fishes. *M. pyrifera* reduces current velocity (Jackson and Winant, 1983) and transit time across a reef that may result in increased settlement of fishes (Carr, 1994a) in transition from a pelagic to benthic existence, and also influences the survival of fishes for some period of time (recruitment) by providing refuges from predators (Anderson, 2001; Johnson, 2006; Steele and Anderson, 2006). Moreover, the specific relationships between fishes and *M. pyrifera* often reflect differential responses to structural components (Carr, 1991; Anderson, 1994) and differential relationships to the density of *M. pyrifera* (Carr, 1994b).

Experimental manipulations of *M. pyrifera* forests have confirmed observational studies (Ebeling et al., 1980; Larson and DeMartini, 1984; DeMartini and Roberts, 1990; Holbrook et al., 1990; Schmitt and Holbrook, 1990) that *M. pyrifera* influences recruitment and the abundance of juvenile and adult reef fishes. Complete removals of *M. pyrifera* forests have resulted in large reductions of several fishes (Bodkin, 1988; Carr, 1989) and an increase in fishes associated with benthic foliose algae that occurs where *M. pyrifera* has been removed (Carr, 1989). What has not been explored, however, is the effect of partial removals through thinning of *M. pyrifera* that serves as a proxy for a gradient in disturbance. Such disturbances, ranging from storm activity and herbivory to human influences result in lower densities of *M. pyrifera*. In addition, there are fundamental differences in mature (bundles of fronds corresponding to older individuals) vs. recovering (dispersed fronds of young individuals) kelp forests that may reveal differential responses of fishes to structural habitat complexity as a result of disturbance.

The goals of this study were to explore the effects of a gradient of local disturbance and subsequent recovery of *M. pyrifera* on the recruitment and abundance of temperate zone rocky reef fishes. We conducted experimental studies over a 3-yr period to address the following questions: (1) How does the loss of *M. pyrifera* by differential thinning affect recruitment and the abundance of juvenile and adult fishes?; (2) Over what time period of recovery will disturbed areas of *M. pyrifera* become similar in recruitment and the abundance of older life stages of fishes to undisturbed kelp forests?; (3) Which attributes of the structure of *M. pyrifera* in mature vs. recovering kelp forests cause differential recruitment of fishes?

## 2. Methods

### 2.1. Study System

This study was conducted at Santa Catalina Island near the Wrigley Marine Science Center located approximately 40 km west of Los Angeles, California (WMSC; 33° 27' N, 118° 29' W). Santa Catalina

Island slopes steeply underwater, with rocky reefs that support large stands of *M. pyrifera*. The similar widths of these kelp forests along the shoreline make them amenable to simulating gradients of disturbance to kelp forests by creating treatments that are of similar size. We identified three sites within a range of 10 km with reefs of *M. pyrifera* sufficient in length and continuity to perform manipulations simulating disturbance: Emerald Bay, West Quarry, and Cliffs (Fig. 1a).

### 2.2. *M. pyrifera* disturbance and recovery: a large-scale experiment

#### 2.2.1. Experimental design

Experimental manipulations at sites along the northeastern side of Santa Catalina Island were conducted in March and June 2005. At each site, a meter tape was deployed parallel to the shoreline at a depth of ~13 m. Twenty-meter long experimental sections were marked with flagging tape, interspersed by 15 m long sections from which all kelp was removed. These "clearings" were established to reduce as much as possible any movement of post-settlement young fishes among treatments of kelp thinning. It was recognized that older juvenile and adult fishes were free to move among treatments, but fish densities in the established treatments may represent potential differences in their distribution caused by habitat preferences as a result of disturbance to the kelp forest ecosystem. At the edge of each treatment, a meter tape was laid perpendicular to shore from the offshore to inshore edge of the

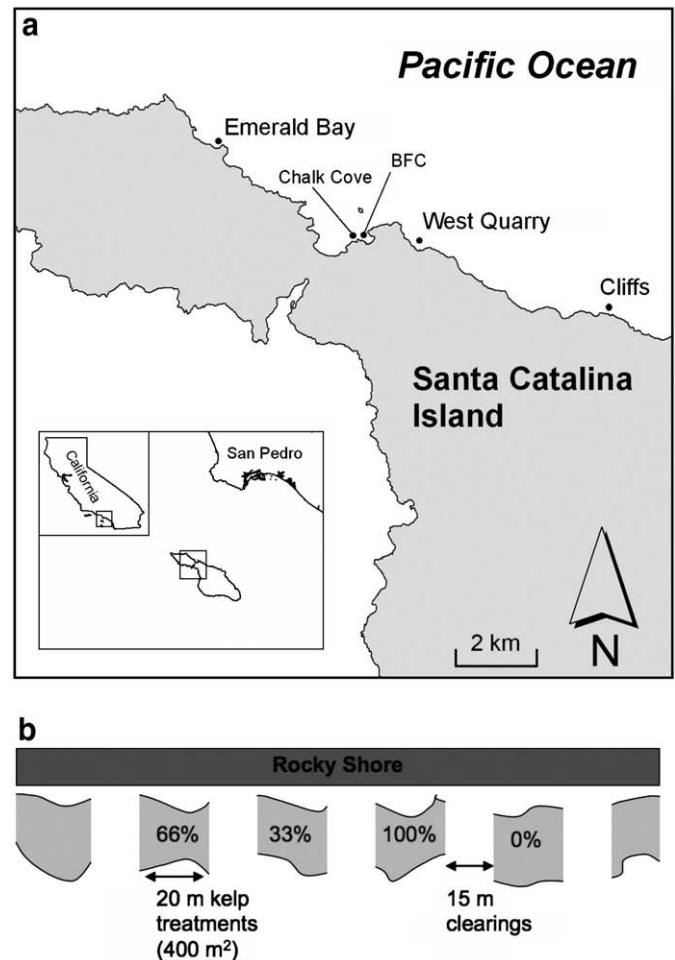


Fig. 1. (a) Map showing Santa Catalina Island, California, and three study sites (Emerald Bay, Cliffs, and West Quarry) used in simulating a gradient in disturbance of kelp forests. Two other sites, Chalk Cove and Big Fisherman Cove (BFC), were used in simulating mature vs. recovering kelp forests. (b) Example of the experimental design in establishment of treatments of kelp removal at one site on Santa Catalina Island. Percentages represent the amount of kelp remaining after manipulation.

kelp forest to assist in clearing between adjacent treatments. Four treatments, each  $\sim 20 \text{ m} \times 20 \text{ m}$ , were established at each of the three experimental sites in a complete randomized block design. The treatments corresponded to 0%, 33%, and 66% of remaining *M. pyrifera* individuals (established by cutting the complementary percentage of the holdfasts in a treatment) and 100% as an unmanipulated control (Fig. 1b). *M. pyrifera* was removed by cutting below the primary dichotomy, just above the holdfast. At the beginning of the subsequent field seasons in 2006 and in 2007, all new growth of macroalgae that occurred in the clearings between treatments was removed.

### 2.2.2. Densities of *M. pyrifera*

To determine whether manipulations simulating kelp forest disturbance corresponded to expected relative densities of *M. pyrifera* and to follow its recovery, surveys of this macroalga were conducted in all treatments and sites in July or August from 2005 to 2007. The density of adults (individuals with at least four fronds  $> 1 \text{ m}$  in height), juveniles (individuals with less than four fronds), and recruits (individuals with one blade and a single stipe) were estimated using counts in ten  $4 \text{ m}^2$  quadrats within each kelp treatment. A meter tape was extended at 13 m depth parallel to the shoreline along the bottom of a treatment, and two-meter tapes were run perpendicularly towards shore from two random points. Five points were randomly selected along either side of these transects to place a quadrat, and the number of individuals and stipes per individual were counted as estimates of the density of *M. pyrifera*.

### 2.2.3. Densities of older juvenile and adult fishes

The densities of juvenile (1-year old or older) and adult fishes (generally  $> 100 \text{ mm}$  total length (TL); see Galst and Anderson, 2008) were estimated in each kelp thinning treatment at each site using belt transects. We grouped these two life stages of fishes together because observations of fishes did not reveal distinct differences in habitat use between them. A baseline meter tape was extended parallel to the shore along the outer edge of the kelp forest at 13 m depth. Two random points within 0–10 m on the first section of the meter tape and another two points within 11–20 m were selected, from which four transects were surveyed perpendicular to shore in midwater and along the reef bottom, with at least 4 m between adjacent transects. An observer first would ascend to midwater (half way between the sea surface and reef bottom) and swim slowly and consistently towards shore, visualizing a 2-m wide  $\times$  2-m high corridor until reaching the inner edge of the kelp forest. Upon reaching the inner edge of the kelp forest ( $\sim 3\text{--}4 \text{ m}$  depth), the observer descended directly below to the reef bottom and repeated the same procedure, swimming along the bottom returning to the baseline transect tape. All fishes observed were recorded by species and size.

In addition to numerical densities of older juvenile and adult fishes, our intent in estimating the size (cm total length; TL) of fishes in situ was to determine whether there were relative differences in biomass densities (e.g., Anderson et al., 1989; Demartini et al., 1989) among treatments and sites. Prior to estimating fish size for data collection purposes, two observers practiced estimating the length of stationary objects relative to actual length, and then together, practiced estimating the lengths of individual fish and reconciled these estimates until both observers recorded lengths of fish within 1 cm of each other. The same two observers collected all data throughout the three-year study to minimize observer bias.

During this survey, a meter tape was extended along the bottom to determine the approximated lengths of the midwater and bottom transects to estimate the volume sampled and the density of fishes. Thus, eight transects were sampled for each treatment, four in midwater and four along the reef bottom. All surveys were conducted between 0830 and 1630 Pacific Daylight Savings Time, and horizontal visibility always exceeded 5 m. Two such surveys across all sites were conducted in July and August 2005, June and August 2006, and June

and July 2007. Due to a landslide that impacted the Cliffs site, this site was not surveyed in 2007.

### 2.2.4. Densities of recruit fishes

We defined recruit fishes as individuals within a size range of 20–80 mm TL that had settled within the current summer and survived for up to 4 months. The densities of recruits were estimated using the same techniques as those for older juvenile and adult fishes but with several modifications. For each of the four transects conducted within each treatment, three depth strata were employed; the kelp canopy ( $\sim 2 \text{ m}$  depth), midwater, and the reef bottom. This design ensured that we would sample recruits of different species that occur in different depth strata within kelp forests (e.g., Anderson, 1994; Carr, 1994a). An observer first began a survey to record the species and size of recruits in the kelp canopy by slowly swimming from the outer edge of the kelp forest towards shore until reaching the inner edge of the kelp forest. Once the inner edge of the kelp forest was reached, the observer descended to midwater and swam back to the baseline meter tape, again recording the species and size of recruits. At that point, the observer descended further to the reef bottom and recorded recruits while swimming back towards shore. Concurrently, a meter tape was extended along the bottom during this transect to measure the approximate length of the canopy, midwater, and bottom transects to estimate the volume sampled. Transect dimensions were 1-m wide  $\times$  1-m high because of the smaller sizes and greater difficulty in detecting recruits within the kelp foliage. Transects were also conducted more slowly than for older life stages of fishes because considerable time was spent searching for recruits in the fronds of *M. pyrifera*. Surveys were conducted in each of three months across sites from 2005 to 2007 (July, August, October 2005; June–August 2006; and June–August 2007). As with older life stages, the Cliffs site was not surveyed in 2007.

### 2.2.5. Analyses

To estimate the density of *M. pyrifera*, counts of stipes were summed across all quadrats within each kelp thinning treatment to obtain the density of stipes per  $40 \text{ m}^2$ . A one-way blocked ANOVA was used to determine whether there were significant differences in the density of *M. pyrifera* among treatments for each year with site used as the blocking factor. Fisher's LSD pairwise comparison tests were used to detect differences between disturbance treatments in the density of *M. pyrifera* stipes for each year separately (Edwards, 1998). Both the lack of a significant difference in the density of stipes among treatments after disturbance (2005), and the density of stipes relative to control treatments (no removal of *M. pyrifera*) were used as evidence of whether *M. pyrifera* had recovered to pre-manipulation densities.

The older life stages of six species of fish were examined for differences among treatments and sites: *Chromis punctipinnis* (Cooper), *Hypsypops rubicundus* (Girard) *Paralabrax clathratus* (Girard), *Brachyistius frenatus* (Gill), *Halichoeres semicinctus* (Ayres), and *Oxyjulis californica* (Günther). Recruits of four species also were analyzed: *C. punctipinnis*, *P. clathratus*, *B. frenatus*, and *O. californica*. These species and life stages had sufficient densities for meaningful statistical analysis. The densities of older life stages and recruits for a given survey and site were standardized to no. per  $100 \text{ m}^3$  within each depth stratum sampled and then averaged across strata for a given transect. Densities were then averaged among the four transects in a given treatment. To obtain overall densities of fishes by treatment and site over a single summer, the estimates of density within treatments were averaged across multiple surveys. For recruits, only surveys in which a species was present were used in estimates of density to account for differences in timing of settlement of fishes to kelp forests. Biomass densities for older life stages of all six species were estimated for numerical densities using known length–weight relationships (DeMartini et al., 1994; Cailliet et al., 2000).

We used one-way blocked ANOVAs to determine whether there were significant differences in the densities of fishes among treatments for each year, with site used as the blocking factor. Data were log-transformed ( $\log[x + 1]$ ) to meet the assumption of homogeneity of variances among treatments. For cases in which site was not significant, the data for each treatment were pooled to conduct a one-way ANOVA with the site variable removed to determine if densities were significantly different among treatments. Fisher's LSD pairwise comparison test was used to determine which treatments differed in density for each year separately (Edwards, 1998). A lack of a significant difference in the density of fishes among kelp treatments, in combination with densities of *M. pyrifera* that had reached or surpassed pre-manipulation densities of stipes was interpreted as recovery in both the density of older fishes and recruitment after initial disturbance. All analyses were conducted using SYSTAT (version 10.3).

### 2.3. Recruitment in mature vs. recovering *M. pyrifera* forests

#### 2.3.1. Experimental design

We conducted an experiment in 2006 to evaluate the relative importance of the distribution and morphology of fronds that represent mature vs. recovering *M. pyrifera* forests following a disturbance in the recruitment of kelp-associated fishes. To provide data on relative differences in the distribution of *M. pyrifera*, we examined the number of stipes per individual (including adult and juvenile life stages) in kelp treatments after disturbance in 2005 (see large-scale experiment). To determine whether there were significant differences in morphology between adult and juvenile *M. pyrifera*, 1-m lengths of *M. pyrifera* were sampled from fronds collected at three reefs along the northeastern side of Santa Catalina Island. After collection, fronds were stored in bins filled with seawater and transported to the laboratory where measurements were recorded. A total of 73 juvenile and 70 adult sections of *M. pyrifera* fronds were collected in summer 2006 and 2007 from similar depths at ~2 m above the sea floor. All fronds were measured for stipe diameter (mm), wet biomass (kg/m of frond), blade area (cm<sup>2</sup>; length × width of two blades), and distance between blades (cm; two distances per frond).

Three treatments were created to investigate the influence of frond distribution and morphology on the recruitment of fishes: adult individuals, juveniles gathered in bundles, and dispersed juvenile *M. pyrifera*, with all treatments standardized to an equivalent number of 30–32 fronds. Six plots consisting of 4 m<sup>2</sup> PVC frames covered with 2.2 cm plastic mesh were constructed for each treatment, divided equally between Big Fisherman Cove (BFC) and Chalk Cove (Fig. 1a) in a complete randomized block design with equal number of treatments in each cove and at each depth. *M. pyrifera* was translocated from nearby reefs and attached to the plastic mesh on PVC frames anchored to the sand bottom. The first treatment involved attaching two adult *M. pyrifera* to the PVC frames, randomly picking two corners of the frame for attachment. Individual *M. pyrifera* modified to 16 stipes per individual were used, approximating the mean number of stipes per individual recorded in kelp control treatments in 2005 ( $17.4 \pm 3.3$  stipes per individual). For the second treatment, fronds from juvenile *M. pyrifera* were tied in bundles of 16 fronds each to simulate the distribution of adult fronds, but also to retain any differences in morphology between adult and juvenile *M. pyrifera*. To simulate recovery of a *M. pyrifera* forest, a third treatment of juvenile *M. pyrifera* (1–3 stipes per individual) was created in which 16 individuals were tied uniformly to plastic mesh attached to the PVC frame. All plots were positioned at least 10 m from each other or from a natural reef. After initiating the experiment on 16 Jul 2006, plots were surveyed for recruits after a 2-week period by gently moving fronds while ascending slowly in the water column to record the species and number of recruits present.

#### 2.3.2. Analyses

To estimate the number of stipes per individual of *M. pyrifera* in treatments of the large-scale experiment, counts of juvenile and adult stipes were summed across all quadrats for each treatment and then divided by the sum of the number of individuals of both life stages. Differences in the number of stipes per individual *M. pyrifera* among treatments and sites were examined with a one-way blocked ANOVA. Student's *t*-tests were used to determine whether there were differences between juvenile and adult fronds of *M. pyrifera* in blade area, distance between blades, stipe diameter, and biomass. We reported separate variance *t* values for all *t*-tests as a conservative approach for analyzing small data sets or uneven sample sizes to avoid incorrectly rejecting the null hypothesis (Ott and Longnecker, 2001). To compare recruitment of fishes among treatments of bundled and dispersed fronds, the number of recruits among treatments and sites were analyzed with a one-way blocked ANOVA. Data were log-transformed ( $\log [x + 1]$ ) to meet the assumption of homogeneity of variances among treatments.

## 3. Results

### 3.1. *M. pyrifera* disturbance, recovery, and fish density

In presenting these results, 0%, 33%, 66%, and 100% (control) kelp denotes the amount of *M. pyrifera* remaining in each treatment after the initial removal of individuals just above the holdfast in 2005. As expected, the density of adult *M. pyrifera* stipes was significantly different among all kelp thinning treatments in 2005 and among sites (treatment:  $F_{3,6} = 31.56$ ,  $p < 0.001$ ; site:  $F_{2,6} = 28.31$ ,  $p = 0.001$ ). Stipe densities (mean  $\pm$  1 SE) of *M. pyrifera* among treatments were  $31.00 \pm 31.00$  (0% kelp remaining),  $86.00 \pm 54.56$  (33% kelp),  $148.67 \pm 44.41$  (66% kelp), and  $243.76 \pm 48.48$  (100% kelp). There was a higher density of *M. pyrifera* at Emerald Bay than at other sites. There were no differences, however, for juvenile ( $F_{3,6} = 0.82$ ,  $p = 0.53$ ) and recruit ( $F_{3,6} = 1.90$ ,  $p = 0.23$ ) *M. pyrifera* among treatments in 2005, although differences were observed among sites (juvenile:  $F_{2,6} = 5.74$ ,  $p = 0.04$ ; recruit:  $F_{2,6} = 5.12$ ,  $p = 0.05$ ).

In general, older juvenile and adult fishes exhibited greater responses in numerical density than recruits to the disturbance of *M. pyrifera*. There were significant differences in the density of *C. punctipinnis* ( $p = 0.03$ ), *P. clathratus* ( $p < 0.001$ ), *B. frenatus* ( $p = 0.003$ ), and all species combined ( $p = 0.009$ ) among treatments (Table 1). *C. punctipinnis* had a higher density in 66% kelp than in 0% kelp and the control, but not in 33% kelp (Fig. 2a). The density of *P. clathratus* was lower in 0% kelp than in all other treatments, and the densities in 33% and 66% kelp were lower than in the control (Fig. 2b). For *B. frenatus*, the density in 0% kelp was lower than in 33% and 66% kelp and the control, and the density in 33% kelp was lower than the control (Fig. 2c). All species combined had a higher density in 66% kelp than in 0% and 33% kelp, but not in the control, and the density in 100% kelp was greater than in 33% kelp (Fig. 2d). There was no significant difference in density among treatments for older juvenile and adult *H. rubicundus*, *H. semicinctus*, and *Oxyjulis californica* (Table 1).

There also were significant differences among sites for *C. punctipinnis*, *H. rubicundus*, *P. clathratus*, *H. semicinctus*, and all species combined (Table 1). *C. punctipinnis*, *H. rubicundus*, and all species combined had higher densities at Cliffs and West Quarry than at Emerald Bay, while *P. clathratus* and *H. semicinctus* had higher densities at Cliffs than at West Quarry, but densities at both sites were not different from those at Emerald Bay.

Treatments of *M. pyrifera* removal had little effect on the biomass density of fishes in 2005. Both *P. clathratus* and *B. frenatus* showed a lower biomass density in 0% kelp than in other treatments ( $p = 0.005$  and  $p = 0.017$ , respectively), and there were no other significant effects of *M. pyrifera* removal treatment on biomass density of fishes in 2005 (Table 1), although differences were observed between sites for *C. punctipinnis*, *H. rubicundus*, and all species combined (Table 1).

**Table 1**

Results of one-way blocked ANOVAs to determine differences in numerical density and biomass density ( $\log[x + 1]$ ) of older life stages of fishes and numerical density of recruits among kelp removal treatments and sites in 2005 (\* = significant difference at  $p \leq 0.05$ ).

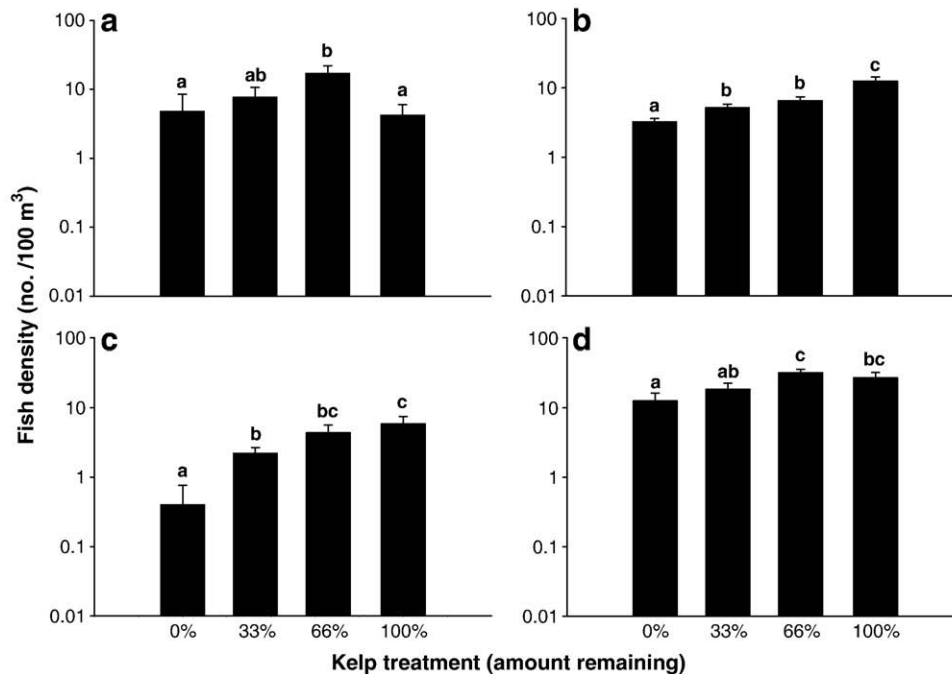
	Species	Treatment	Site
Older fishes-numerical density	<i>C. punctipinnis</i>	$F_{3,6} = 6.50, p = 0.03^*$	$F_{2,6} = 11.28, p = 0.009^*$
	<i>H. rubicundus</i>	$F_{3,6} = 0.49, p = 0.70$	$F_{2,6} = 48.52, p < 0.001^*$
	<i>P. clathratus</i>	$F_{3,6} = 38.71, p < 0.001^*$	$F_{2,6} = 6.03, p = 0.04^*$
	<i>B. frenatus</i>	$F_{3,8} = 11.31, p = 0.003^*$	NS
	<i>H. semicinctus</i>	$F_{3,6} = 1.20, p = 0.39$	$F_{2,6} = 5.02, p = 0.05^*$
	<i>O. californica</i>	$F_{3,6} = 1.98, p = 0.22$	$F_{2,6} = 0.87, p = 0.47$
	All species combined	$F_{3,6} = 10.33, p = 0.009^*$	$F_{2,6} = 7.95, p = 0.02^*$
Older fishes-biomass density	<i>C. punctipinnis</i>	$F_{3,6} = 3.76, p = 0.08$	$F_{2,6} = 9.13, p = 0.02^*$
	<i>H. rubicundus</i>	$F_{3,6} = 0.11, p = 0.95$	$F_{2,6} = 16.35, p = 0.004^*$
	<i>P. clathratus</i>	$F_{3,6} = 12.51, p = 0.005^*$	$F_{2,6} = 2.01, p = 0.21$
	<i>B. frenatus</i>	$F_{3,6} = 7.88, p = 0.017^*$	$F_{2,6} = 0.73, p = 0.52$
	<i>H. semicinctus</i>	$F_{3,6} = 1.09, p = 0.42$	$F_{2,6} = 2.67, p = 0.15$
	<i>O. californica</i>	$F_{3,6} = 0.58, p = 0.65$	$F_{2,6} = 0.62, p = 0.57$
	All species combined	$F_{3,6} = 0.42, p = 0.75$	$F_{2,6} = 24.03, p = 0.001^*$
Recruit fishes	<i>C. punctipinnis</i>	$F_{3,6} = 0.68, p = 0.59$	$F_{2,6} = 2.04, p = 0.21$
	<i>P. clathratus</i>	$F_{3,6} = 2.04, p = 0.21$	$F_{2,6} = 0.22, p = 0.81$
	<i>B. frenatus</i>	$F_{3,6} = 6.62, p = 0.03^*$	$F_{2,6} = 5.66, p = 0.04^*$
	<i>O. californica</i>	$F_{3,6} = 3.30, p = 0.10$	$F_{2,6} = 0.62, p = 0.57$
	All species combined	$F_{3,6} = 1.48, p = 0.31$	$F_{2,6} = 0.148, p = 0.30$

Surprisingly, only *B. frenatus* showed differences in the density of recruits among kelp treatments ( $p = 0.03$ , Table 1, Fig. 3a), while *O. californica* exhibited a near-significant pattern of higher densities in less disturbed kelp treatments ( $p = 0.10$ , Table 1, Fig. 3b). The density of *B. frenatus* in 0% kelp was less than in 66% kelp and the control, and the density in 33% kelp was less than the control. *B. frenatus* also had a lower density of recruits at Cliffs than at Emerald Bay (Table 1). There was no difference in the density of *C. punctipinnis*, *P. clathratus* or all species combined among treatments or sites (Table 1).

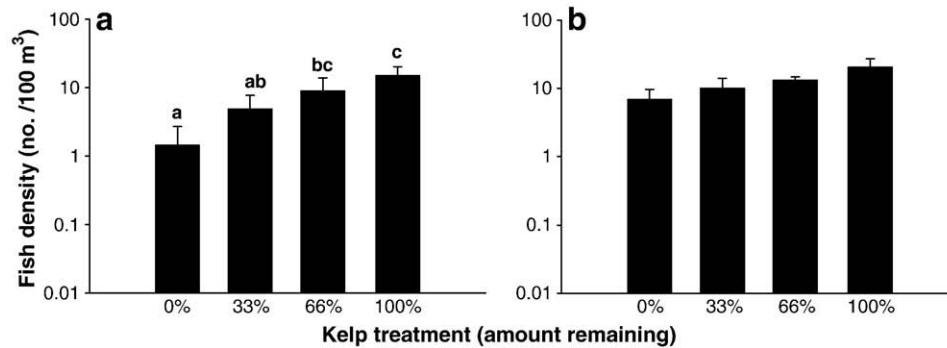
All species of fishes examined for differences in density among kelp thinning treatments for the initial disturbance in 2005 were also examined in the following two years in testing for the effects of *M. pyrifera* recovery on the densities of fishes. For all older life stages of six fish species and for all of these species combined, there was no difference in the numerical density of fishes among treatments in

2006 or 2007 (Table 2). For fish recruits, there was no difference in their densities among treatments or sites after 2005 (Table 2). As in 2005, there was a near-significant difference among treatments in the abundance of *O. californica* recruits in 2006 (Table 2), with a similar pattern of increasing densities with less *M. pyrifera* removed. Biomass density showed a similar response to recovery as numerical density, with all but one species showing no effect of kelp treatment on the biomass densities of fishes in 2006 or 2007 (Table 2). *H. semicinctus* showed lower biomass densities in the 0% kelp than the 66% kelp and control in 2007 ( $p = 0.05$ ). There were differences in biomass densities among sites for *H. rubicundus*, *P. clathratus*, *B. frenatus*, *H. semicinctus*, *O. californica*, and all species combined in 2006, and for *H. rubicundus*, and all species combined in 2007 (Table 2).

After 2005, there was no difference in the density of *M. pyrifera* among treatments in subsequent years (Table 2, Fig. 4). Densities



**Fig. 2.** Mean densities ( $\pm 1$  SE) of older life stage fishes among treatments of kelp disturbance in 2005: (a) *C. punctipinnis*, (b) *P. clathratus*, (c) *B. frenatus*, and (d) all species combined. Percentages denote the amount of *M. pyrifera* remaining after kelp removal. Treatments with different letters are significantly different from each other.



**Fig. 3.** Mean densities ( $\pm$  1SE) of recruit fishes among treatments of kelp disturbance in 2005: (a) *B. frenatus*, and (b) *O. californica*. Percentages denote the amount of *M. pyrifera* remaining after kelp removal. Treatments with different letters are significantly different from each other.

became more uniform across sites in 2006, and this trend continued into 2007. There was a significant increase in total stipe density between 2005 and 2006 ( $F_{2,29} = 6.60$ ,  $p = 0.004$ ), with similar densities in 2007 as in 2006, indicating that the density of *M. pyrifera* returned to pre-manipulation densities.

### 3.2. Recruitment in mature vs. recovering *M. pyrifera* forests

Based on surveys of *M. pyrifera* in 2005, not only were there differences in stipe density among areas, but there was a strong trend for differences in the number of stipes per individual of *M. pyrifera* with lower densities in the 0% and 33% kelp treatments than the 66% and 100% kelp ( $F_{3,6} = 3.82$ ,  $p = 0.08$ ; Fig. 5a). Stipe diameter ( $t = 15.16$ ,  $p < 0.001$ ; Fig. 5b) and frond biomass ( $t = 6.38$ ,  $p < 0.001$ ; Fig. 5c) were greater for adult *M. pyrifera* than for juveniles, and there was a strong trend for larger blade area in adults ( $t = 1.85$ ,  $p = 0.07$ ; Fig. 5d). Also reflecting lower biomass in juvenile *M. pyrifera*, the distance between blades was greater for juveniles than adults ( $t = -6.50$ ,  $p < 0.001$ ; Fig. 5e).

There was no difference in recruitment of fishes to treatments simulating mature vs. recovering *M. pyrifera* forests between sites ( $p = 0.69$ ). Therefore, data were pooled to conduct a one-way ANOVA to determine whether there were differences among treatments ( $n = 6$ ). Recruitment of kelp-associated fishes (*P. clathratus* and *O. californica* combined) after 2 weeks was significantly higher on adult *M. pyrifera* and bundled fronds of juvenile *M. pyrifera* than on a dispersed distribution of juvenile *M. pyrifera*, indicating that the

distribution of fronds vs. their morphology primarily influences recruitment ( $F_{2,15} = 7.07$ ,  $p = 0.007$ ; Fig. 6).

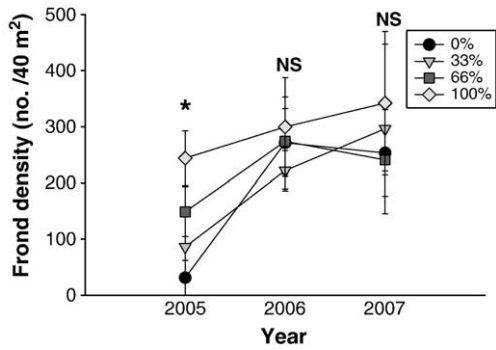
## 4. Discussion

There is ample evidence that macroalgae influence the distribution and abundance of temperate reef fishes (Choat and Ayling, 1987; Jones, 1988; Ebeling and Hixon, 1991; Stephens et al., 2006). In particular, both observational (Ebeling et al., 1980; Larson and DeMartini, 1984; DeMartini and Roberts, 1990; Holbrook et al., 1990) and experimental (Bodkin, 1988; Carr, 1989) evidence suggest that the amount and structural habitat complexity of kelps influences recruitment success and the density of rocky reef fishes. Few studies (Carr, 1994a), however, have examined experimentally the relationships between the densities or other habitat attributes of kelps and the densities of fishes.

A stronger response to variation in disturbance was observed among older life stage fishes than for recruits of these species. The density of adult *P. clathratus* was strongly and positively related to variation in the density of *M. pyrifera*, a result similar to what has been observed in previous studies (Carr, 1989; Holbrook et al., 1990). Interestingly, however, the density of *P. clathratus* at intermediate levels of disturbance (33% and 66% kelp remaining), was significantly different from both the control and total removal of *M. pyrifera*. These differences, which would not have been detected with manipulations only of the presence and absence of *M. pyrifera* (Bodkin, 1988; Carr,

**Table 2**  
Results of one-way blocked ANOVAs for 2006 (3 sites) and 2007 (2 sites) on the effect of *M. pyrifera* treatment and site on the numerical and biomass densities ( $\log(x + 1)$ ) of older life stages of fishes, and numerical density of recruits, and adult *M. pyrifera* (\* = significant difference at  $p \leq 0.05$ ).

	Species	2006-Treatment	2006-Site	2007-Treatment	2007-Site	
Older fishes-numerical density	<i>C. punctipinnis</i>	$F_{3,6} = 2.94$ , $p = 0.12$	$F_{2,6} = 1.40$ , $p = 0.32$	$F_{3,3} = 0.30$ , $p = 0.82$	$F_{1,3} = 0.90$ , $p = 0.41$	
	<i>H. rubicundus</i>	$F_{3,6} = 0.66$ , $p = 0.33$	$F_{2,6} = 7.48$ , $p = 0.84$	$F_{3,3} = 2.21$ , $p = 0.27$	$F_{1,3} = 79.04$ , $p = 0.003^*$	
	<i>P. clathratus</i>	$F_{3,6} = 2.0$ , $p = 0.22$	$F_{2,6} = 4.99$ , $p = 0.05^*$	$F_{3,3} = 2.21$ , $p = 0.27$	$F_{1,3} = 18.23$ , $p = 0.02^*$	
	<i>B. frenatus</i>	$F_{3,6} = 1.11$ , $p = 0.42$	$F_{2,6} = 3.69$ , $p = 0.09$	$F_{3,3} = 2.01$ , $p = 0.29$	$F_{1,3} = 0.003$ , $p = 0.96$	
	<i>H. semicinctus</i>	$F_{3,6} = 0.98$ , $p = 0.46$	$F_{2,6} = 2.59$ , $p = 0.16$	$F_{3,3} = 1.76$ , $p = 0.33$	$F_{1,3} = 0.05$ , $p = 0.84$	
	<i>O. californica</i>	$F_{3,6} = 1.04$ , $p = 0.44$	$F_{2,6} = 4.34$ , $p = 0.07$	$F_{3,3} = 0.36$ , $p = 0.79$	$F_{1,3} = 0.84$ , $p = 0.43$	
	All species combined	$F_{3,6} = 1.39$ , $p = 0.33$	$F_{2,6} = 0.38$ , $p = 0.70$	$F_{3,3} = 0.20$ , $p = 0.89$	$F_{1,3} = 10.01$ , $p = 0.05^*$	
	Older fishes-biomass density	<i>C. punctipinnis</i>	$F_{3,6} = 1.87$ , $p = 0.24$	$F_{2,6} = 0.95$ , $p = 0.44$	$F_{3,3} = 0.45$ , $p = 0.74$	$F_{1,3} = 0.85$ , $p = 0.42$
		<i>H. rubicundus</i>	$F_{3,6} = 1.14$ , $p = 0.41$	$F_{2,6} = 11.19$ , $p = 0.009^*$	$F_{3,3} = 1.24$ , $p = 0.43$	$F_{1,3} = 26.62$ , $p = 0.01^*$
		<i>P. clathratus</i>	$F_{3,6} = 0.41$ , $p = 0.75$	$F_{2,6} = 5.54$ , $p = 0.04^*$	$F_{3,3} = 5.12$ , $p = 0.11$	$F_{1,3} = 1.14$ , $p = 0.36$
<i>B. frenatus</i>		$F_{3,6} = 0.63$ , $p = 0.62$	$F_{2,6} = 4.86$ , $p = 0.06$	$F_{3,3} = 1.04$ , $p = 0.49$	$F_{1,3} = 0.09$ , $p = 0.79$	
<i>H. semicinctus</i>		$F_{3,6} = 2.07$ , $p = 0.21$	$F_{2,6} = 5.66$ , $p = 0.04^*$	$F_{3,3} = 9.94$ , $p = 0.05^*$	$F_{1,3} = 0.55$ , $p = 0.51$	
<i>O. californica</i>		$F_{3,6} = 0.60$ , $p = 0.64$	$F_{2,6} = 7.36$ , $p = 0.02^*$	$F_{3,3} = 0.57$ , $p = 0.67$	$F_{1,3} = 1.82$ , $p = 0.27$	
All species combined		$F_{3,6} = 0.97$ , $p = 0.47$	$F_{2,6} = 13.09$ , $p = 0.006^*$	$F_{3,3} = 0.75$ , $p = 0.59$	$F_{1,3} = 16.35$ , $p = 0.03^*$	
Recruit fishes		<i>C. punctipinnis</i>	$F_{3,6} = 0.15$ , $p = 0.93$	$F_{2,6} = 1.16$ , $p = 0.38$	$F_{3,3} = 2.32$ , $p = 0.25$	$F_{1,3} = 17.02$ , $p = 0.03^*$
		<i>P. clathratus</i>	$F_{3,6} = 2.23$ , $p = 0.25$	$F_{2,6} = 1.22$ , $p = 0.36$	NA	NA
		<i>B. frenatus</i>	$F_{3,6} = 1.16$ , $p = 0.40$	$F_{2,6} = 0.41$ , $p = 0.68$	$F_{3,3} = 0.31$ , $p = 0.82$	$F_{1,3} = 45.24$ , $p = 0.007^*$
	<i>O. californica</i>	$F_{3,6} = 4.38$ , $p = 0.06$	$F_{2,6} = 20.64$ , $p = 0.002^*$	$F_{3,3} = 0.61$ , $p = 0.65$	$F_{1,3} = 6.75$ , $p = 0.08$	
	All species combined	$F_{3,6} = 0.18$ , $p = 0.95$	$F_{2,6} = 1.88$ , $p = 0.23$	$F_{3,3} = 1.54$ , $p = 0.37$	$F_{1,3} = 16.15$ , $p = 0.03^*$	
	<i>M. pyrifera</i>	$F_{3,6} = 0.97$ , $p = 0.47$	$F_{2,6} = 14.72$ , $p = 0.005^*$	$F_{3,3} = 0.62$ , $p = 0.65$	$F_{1,3} = 10.32$ , $p = 0.05^*$	



**Fig. 4.** Mean densities ( $\pm$  1SE) of adult *M. pyrifera* stipes over a three-year period, averaged across sites by treatment. There were no significant (NS) differences between treatments after 2005 (\* = significant difference at  $p \leq 0.05$ ).

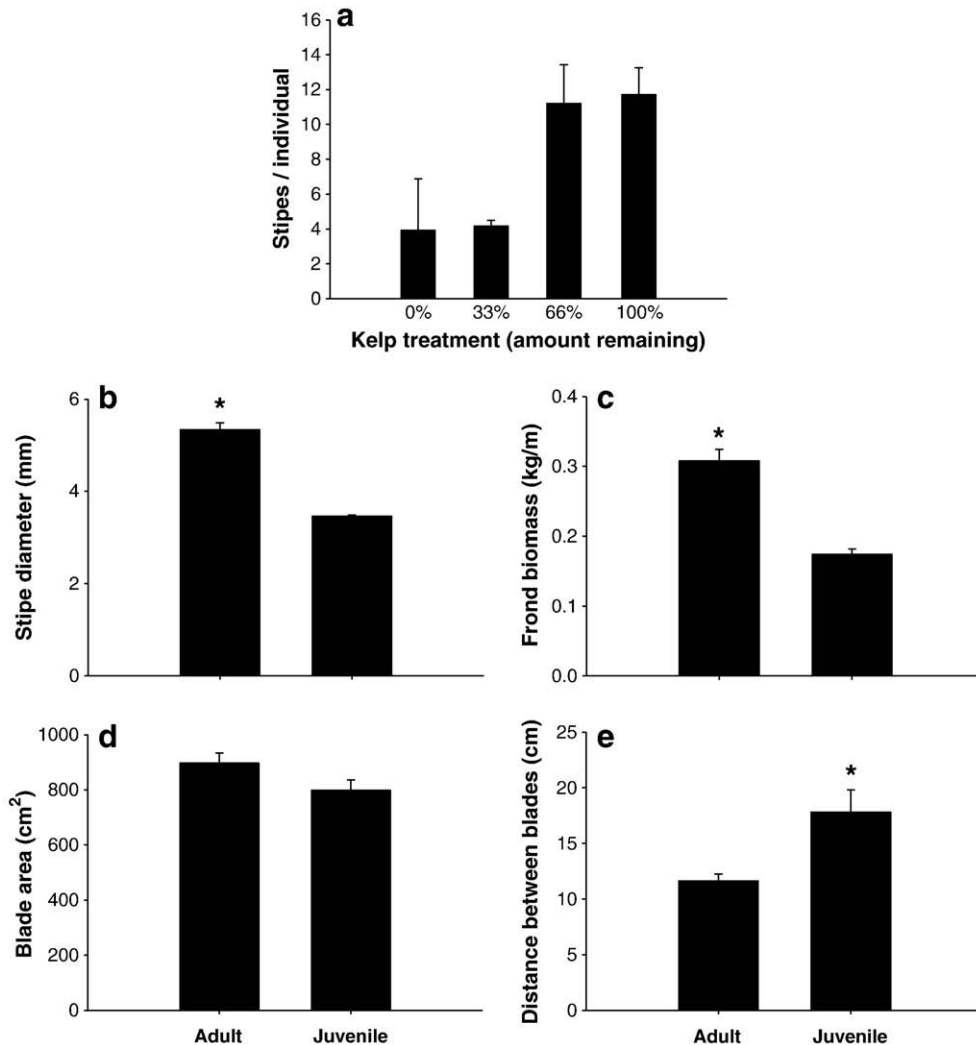
1989) as extremes in disturbance, suggest that responses by fishes to gradients in disturbance reflect the severity and type of disturbance.

Similarly, adult *B. frenatus*, with a strong negative response in their density to total *M. pyrifera* removal (Carr, 1989), had significantly different densities at intermediate levels of disturbance than controls and the total removal of *M. pyrifera*. The density of this species is positively related to the canopy cover, stipe density, and individual density of *M. pyrifera* (Anderson, 1994). The observed decrease in the

density of *B. frenatus* with less *M. pyrifera* is likely due to a loss of both habitat (Anderson, 1994) and food for adults that heavily feed on mesograzers from *M. pyrifera* surfaces (Bray and Ebeling, 1975; Holbrook et al., 1990; Davenport and Anderson, 2007).

Older juvenile and adult *O. californica* did not show a significant response to *M. pyrifera* disturbance, although an increasing trend in their density was observed with higher percentages of the remaining *M. pyrifera* individuals. *O. californica* feed opportunistically on small motile invertebrates associated with the kelp canopy and the benthos and have a greater breadth in habitat than *B. frenatus* (Bray and Ebeling, 1975). Therefore, they may be less impacted by disturbance to kelp forests than other microcarnivorous fishes because they feed on sources of food that are not necessarily associated with kelp. In addition, their aggregating behavior (Bray and Ebeling, 1975) may result in less risk of predation, allowing them to persist in *M. pyrifera* forests with relatively low densities of *M. pyrifera* (Hobson, 1978).

Surprisingly few differences in the abundance of recruits were observed among treatments of *M. pyrifera* disturbance, given the high degree of association of recruit fishes with *M. pyrifera* (Carr, 1989; Holbrook et al., 1990). For example, recruitment of *P. clathratus* did not differ among treatments, despite previous research that suggests that variation in recruitment success of this species is positively related to spatial and temporal variation in the density of *M. pyrifera* at smaller spatial scales (Holbrook et al., 1990; Carr, 1994a). This relationship, however, may be weaker at larger spatial scales or with



**Fig. 5.** Mean ( $\pm$  1SE) of parameters measured for juvenile and adult *M. pyrifera*: (a) stipes per kelp individual (both adults and juveniles) for all treatments in 2005 averaged across sites and (b) stipe diameter, (c) frond biomass, (d) blade area, and (e) distance between blades between individual adult and juvenile kelp (\* = significant difference at  $p \leq 0.05$ ).

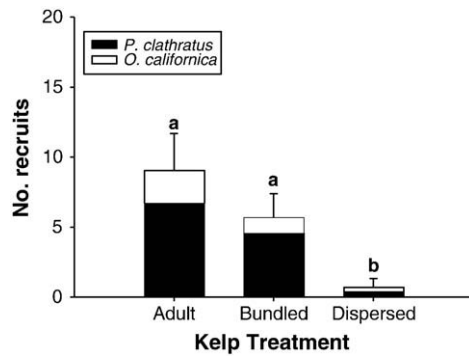


Fig. 6. Mean number ( $\pm$  1 SE) of recruit *P. clathratus* and *O. californica* among treatments comparing the distribution and morphology of adult vs. juvenile *M. pyrifera*. Treatments with different letters are significantly different from each other.

low overall densities of *M. pyrifera* (Steele et al., 2002). Densities of *M. pyrifera* in this study were comparable to those of Carr (1989), but the recruitment of *P. clathratus* in his study was notably two- to four-times higher than in this study, which may have led to the overall lack of a response by recruits of *P. clathratus* to structural habitat complexity. Certainly differences in the densities of recruits with variation in the density of *M. pyrifera* would be more difficult to detect when recruitment of several fishes is relatively low, as observed in this study.

As with adults, we observed a strong positive relationship between young *B. frenatus* and the amount of remaining *M. pyrifera* individuals after the initial disturbance. Juvenile *B. frenatus* are closely associated with the kelp canopy in their first few months of life (Anderson, 1994), and the observed decrease in the density of young *B. frenatus* with increasing simulated disturbance may be due to a loss of structural refuge and increased predation risk (Anderson, 2001), similar to other surfperches (Ebeling and Laur, 1985).

Although no significant differences in the densities of recruit *O. californica* among treatments of *M. pyrifera* removal were observed, there was a general increase in the density of fish with higher percentages of remaining *M. pyrifera* individuals. As with older life stages of this species, recruits of *O. californica* occur in aggregations as recruits, possibly conveying more protection from predators and less reliance on the structural complexity of kelp habitat. It also may be that similar to *P. clathratus*, lower recruitment of *O. californica* in 2005 did not allow us to distinguish clear differences in the density of recruits among treatments.

Fish-habitat relationships are species specific, and it is clear from our findings that the relationships between reef fishes and *M. pyrifera* depend on the association of each species to the structural complexity of this habitat, requirements for food and shelter, and the magnitude of recruitment. Fishes that are more closely associated with *M. pyrifera* are more negatively affected by its removal than species more closely associated with the benthos (Moreno and Jara, 1984; Bodkin, 1988; Carr, 1989). In this study, fishes associated with benthic algae or rocky habitats were less affected by disturbance to *M. pyrifera*. For example, *H. rubicundus*, which uses rocky substratum and benthic algae for food and reproduction (Clarke, 1970; Sikkell, 1995), and *H. semicinctus*, a species associated more with foliose benthic algae than with *M. pyrifera* (Hobson and Chess, 2001), showed no response in differential disturbance treatments of kelp. Similarly, adult *C. punctipinnis*, which feeds on zooplankton in open waters beyond the kelp forest (Bray, 1981), and recruits of this species that are associated closely with rocky substratum (Anderson et al., 1989) did not show a clear response to the removal of *M. pyrifera*. Aggregations of both life stages occur in open areas of the water column, and higher densities of *C. punctipinnis* within treatments of intermediate densities of *M. pyrifera* may be a compromise between predation risk (proximity to kelp structure as shelter) and food availability in feeding on zooplankton

away from kelp structure that may impede current velocity (Jackson and Winant, 1983).

Besides the direct effects of the removal of *M. pyrifera* individuals on fishes, a possible indirect effect is the potential increase in understory foliose algae accompanied by increases in the densities of some fishes. Both surfperches (Embiotocidae: Schmitt and Holbrook, 1990) and kelpfishes (Clinidae: Carr, 1989) may increase in density in response to an increase in understory algae following the removal of *M. pyrifera* forests. Similar effects have been observed with leather-jackets (Monacanthidae) and the damselfish *Parma victoriae* (Pomacentridae) after the experimental removal of the kelp *Ecklonia radiata* in temperate Australia (Jones, 1992). Such indirect effects, however, may vary depending on the recovery rate of kelp following disturbance. No change in the cover of understory foliose algae was observed among treatments or across years in this study (unpublished data), perhaps because the rapid recovery of the kelp canopy within the first year following disturbance did not allow for an increase in understory algae.

Recovery of treatments of *M. pyrifera* removal to pre-manipulation levels occurred within the first year after the initial manipulation. The densities of stipes across treatments and sites showed a significant increase with the first year following disturbance that subsequently did not increase in 2007, suggesting that recovery occurred quickly within the first year. Recovery of *M. pyrifera* is highly dependent on environmental conditions, including ocean temperature, nutrient availability, and storm activity (Gerard, 1982; Tegner and Dayton, 1987). Within normal temperature ranges, full recovery of a decimated *M. pyrifera* forest to a pre-disturbed state can occur within 6–9 months (Ladah et al., 1999). Rapid rates of recovery may occur through recolonization by individual *M. pyrifera* not affected by disturbance, immigration of propagules from more distant sites (Reed et al., 2004), and by the existence of a “seed bank” that may allow microscopic *M. pyrifera* to survive conditions too stressful for the macroscopic stage (Carney and Edwards, 2006), possibly allowing for the recovery of isolated populations. Once established, *M. pyrifera* can grow quickly, reaching an adult stage (at least 4 stipes per individual) within 4 months (Neushul and Haxo, 1963).

Importantly, the recovery of *M. pyrifera* was directly reflected in the density of fishes at our experimental sites. After the initial disturbance in 2005, there were no significant differences in fish density among treatments for both adult and recruit life stages in subsequent years. To our knowledge, this is the first study of post-disturbance recovery of *M. pyrifera* on the abundance of fishes. Our results indicate that in the case of a local disturbance event to a kelp forest ecosystem of a similar size to our experiment (10–100 m), followed by favorable environmental conditions for *M. pyrifera* re-establishment and growth, there will be few if any long-term effects on the density and species composition of associated fishes. However, it is possible that frequent disturbances may lead to greater impacts on fish abundance, depending on the life history characteristics of the species. Fishes that have a pelagic larval stage may be able to recover more quickly from disturbance because replenishment of local populations can occur by arrival of larvae from elsewhere. Live-bearing fishes such as surfperches, however, may experience prolonged impacts because of losses in the local adult population that are the direct source of input of young. It is also possible that there would be a decrease in the number of available juvenile and adult migrants to a disturbed location depending on the spatial scale and duration of the disturbance.

During the process of recovery, fundamental differences in the characteristics of mature vs. recovering *M. pyrifera* forests result in differential recruitment of fishes. In this study, the distribution of fronds is of primary importance to recruitment success of kelp-associated fishes in that bundled fronds had higher recruitment than dispersed fronds. Recruit *P. clathratus* are often found between overlapping blades from neighboring fronds (Carr, 1994a). Recruits of the kelp rockfish

(Serranidae: *Sebastes atrovirens*) occur in higher densities on individual *M. pyrifera* with more stipes, and aggregations of this species appear to be closely associated with bundles of fronds than with individual fronds (Nelson, 2001). The habitat provided by individual fronds, representing a recovering kelp forest, may not offer as much protection from predators as bundles of fronds. The less complex habitat offered by dispersed juvenile kelp may lead to a decrease in visual barriers for predators, which may lead to a higher encounter rate of predators and prey (Savino and Stein, 1982; Persson and Eklov, 1995). Whether differences in recruitment between bundled and dispersed distributions of fronds of *M. pyrifera* is due to habitat selection or differential predation remains to be explored.

Although not significant, somewhat intermediate levels of recruitment were observed on bundled fronds of juvenile *M. pyrifera*, which may indicate that the morphology of *M. pyrifera* may also influence recruitment success. Recruitment of *P. clathratus* may increase rapidly and reach an asymptote with higher stipe densities of *M. pyrifera* (Carr, 1994a), but because of density-dependent growth in *M. pyrifera*, blade biomass is linearly related to recruitment of *P. clathratus*, suggesting that recruitment may be limited by blade surface area and not stipe density. Although we observed a significant difference in the biomass of juvenile and adult fronds of *M. pyrifera*, such a difference did not result in differential recruitment, possibly because frond distribution has an overriding effect on recruitment.

Although there are clear effects of local disturbance on the abundance of kelp forest fishes, recovery of *M. pyrifera* under normal conditions occurs in a relatively short period of time. During recovery, however, differences in the distribution of fronds and perhaps their morphology and biomass, may reveal differential effects on recruitment. The effects of a gradient in local disturbance on kelp-associated fishes ultimately will depend on the type, severity, and frequency of disturbance coupled with the magnitude of recruitment and species-specific fish–habitat relationships.

## Acknowledgements

We thank A. Deza, and T. Goodman for their outstanding assistance in carrying out this research project. We also thank D. Cie, A. Davenport, C. Feist, S. Fejtek, C. Galst, P. Kutchner, L. Lewis, and P. Matson for additional field assistance. This research was conducted in partial fulfillment of a master's degree by K. C. O'Connor, and we thank M. Edwards and D. Stow for their advice and for reviewing this manuscript. We also thank the Wrigley Marine Science Center and associated staff for their assistance and logistical support. This research was supported through grants from the National Undersea Research Program, West Coast and Polar Regions Center (UAF(CA)-03-02), the National Institute for Undersea Science and Technology (05-07-006), and the National Science Foundation (OCE-03-31895) to T.W.A. and from the Hardman Foundation, Mabel Myers Memorial Fund, and San Diego State University Ecology program to K.C.O. This is Contribution No. 243 of the Wrigley Institute for Environmental Studies. [RH]

## References

Anderson, T.W., 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Mar. Ecol. Prog. Ser.* 113, 279–290.

Anderson, T.W., 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82, 245–257.

Anderson, T.W., DeMartini, E.E., Roberts, D.A., 1989. The relationship between habitat structure, body size and distribution of fishes at a temperate artificial reef. *Bull. Mar. Sci.* 44, 681–697.

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

Bray, R.N., 1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *Fish. Bull.* 78, 829–841.

Bray, R.N., Ebeling, A.W., 1975. Food, activity, and habitat of three “picker type” microcarnivorous fishes in the kelp forests off Santa Barbara, California. *Fish. Bull.* 73, 815–829.

Cailliet, G.M., Burton, E.J., Cope, J.M., Kerr, L.A., 2000. Biological characteristics of nearshore fishes of California: A review of existing knowledge and proposed additional studies for the Pacific Ocean Interjurisdictional Fisheries Management Plan Coordination and Development. Submitted to the Pacific States Marine Fisheries Commission.

Carney, L.T., Edwards, M.S., 2006. Cryptic processes in the sea: a review of delayed development in the microscopic life stages of marine macroalgae. *Algae* 21, 161–168.

Carpenter, S., Walker, B., Anderies, M., Abel, N., 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* 4, 765–781.

Carr, M.H., 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *J. Exp. Mar. Biol. Ecol.* 126, 59–76.

Carr, M.H., 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *J. Exp. Mar. Biol. Ecol.* 146, 113–137.

Carr, M.H., 1994a. Effects of macroalgal dynamics on recruitment of a temperate marine fish. *Ecology* 75, 1320–1333.

Carr, M.H., 1994b. Predicting recruitment of temperate reef fishes in response to changes in macrophyte density caused by disturbance. In: Stouder, D.J., Fresh, K.L., Feller, R.J. (Eds.), *Theory and Application of Fish Feeding Ecology*. University of South Carolina Press, Columbia, SC, pp. 255–268.

Carr, M.H., Syms, C., 2006. Recruitment. In: Allen, L.G., Pondella, D.J., Horn, M.H. (Eds.), *The Ecology of Marine Fishes: California and Adjacent Waters*. University of California Press, Berkeley, pp. 411–427.

Carr, M.H., Neigel, J.L., Estes, J.A., Andelman, S., Warner, R.R., Largier, J.L., 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecol. Appl.* 13, S90–S107.

Choat, J.H., Ayling, A.M., 1987. The relationship between habitat structure and fish faunas on New Zealand reefs. *J. Exp. Mar. Biol. Ecol.* 110, 257–284.

Clarke, G.A., 1970. Territorial behaviors and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicundus*. *Ecol. Monogr.* 40, 189–212.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.

Davenport, A.C., Anderson, T.W., 2007. Positive indirect effects of reef fishes on kelp performance: the importance of mesograzers. *Ecology* 88, 1548–1561.

Dayton, P.K., Tegner, M.J., 1984. Catastrophic storms, El Niño, and patch stability and a southern California kelp community. *Science* 224, 283–285.

Dayton, P.K., Curry, V., Gerrodette, T., Keller, B.D., Rosenthal, R., Tresca, D.V., 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* 54, 253–289.

Dayton, P.K., Tegner, M.J., Parnell, P.E., Edwards, P.B., 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62, 421–445.

DeMartini, E.E., Roberts, D.A., 1990. Effects of giant kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. *Bull. Mar. Sci.* 46, 287–300.

DeMartini, E.E., Roberts, D.A., Anderson, T.W., 1989. Contrasting patterns of fish density and abundance at an artificial rock reef and a cobble-bottom kelp forest. *Bull. Mar. Sci.* 44, 881–892.

DeMartini, E.E., Barnett, A.M., Johnson, T.D., Ambrose, R.F., 1994. Growth and production estimates for biomass-dominant fishes on a southern California artificial reef. *Bull. Mar. Sci.* 55, 484–500.

Ebeling, A.W., Hixon, M.A., 1991. Tropical and temperate reef fishes: comparison of community structures. In: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, pp. 509–563.

Ebeling, A.W., Laur, D.R., 1985. The influence of plant cover on surfperch abundance at an offshore temperate reef. *Environ. Biol. Fish.* 12, 169–179.

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

Ebeling, A.W., Laur, D.R., Rowley, R.J., 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Mar. Biol.* 84, 287–294.

Edwards, M.S., 1998. Effects of long-term kelp canopy exclusion on the abundance of the annual algae *Desmarestia ligulata*. *J. Exp. Mar. Biol. Ecol.* 228, 309–326.

Edwards, M.S., 2004. Estimating scale-dependency in disturbance impact: El Niños and giant kelp forests in the northeast Pacific. *Oecologia* 138, 436–447.

Edwards, M.S., Hernandez-Carmona, G., 2005. Delayed recovery of giant kelp near its southern range limit in the north Pacific following El Niño. *Mar. Biol.* 147, 273–279.

Enright, N.J., Lamont, B.B., 1989. Seed banks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *J. Ecol.* 77, 1111–1122.

Galst, C.A., Anderson, T.W., 2008. Fish–habitat associations and the role of disturbance in surfgrass beds. *Mar. Ecol. Prog. Ser.* 365, 177–186.

Gerard, V.A., 1982. Growth and utilization of internal nitrogen reserves by the giant kelp, *Macrocystis pyrifera* in a low nitrogen environment. *Mar. Biol.* 66, 27–35.

Graham, M.H., Harrold, C., Lysin, S., Light, K., Watanabe, J.M., Foster, M.S., 1997. Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. *Mar. Ecol. Prog. Ser.* 148, 269–279.

Hobson, E.S., 1978. Aggregating as a defense against predators in aquatic and terrestrial environments. In: Reese, E.D., Lighter, F.J. (Eds.), *Contrasts in Behavior*. John Wiley & Sons, New York, pp. 219–234.

Hobson, E.S., Chess, J.R., 2001. Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. *Environ. Biol. Fish.* 60, 411–457.

Holbrook, S.J., Carr, M.H., Schmitt, R.J., Coyer, J.A., 1990. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bull. Mar. Sci.* 47, 104–114.

Jackson, G.A., Winant, C.D., 1983. Effect of a kelp forest on coastal currents. *Cont. Shelf Res.* 2, 75–80.

Johnson, D.W., 2006. Density dependence in marine fish populations revealed at small and large spatial scales. *Ecology* 87, 319–325.

Jones, G.P., 1988. Ecology of rocky reef fish of northeastern New Zealand – a review. *N. Z. J. Mar. Freshwat. Res.* 22, 445–462.

- Jones, G.P., 1992. Interactions between herbivorous fishes and macro-algae on a temperate rocky reef. *J. Exp. Mar. Biol. Ecol.* 159, 217–235.
- Keeley, J.E., 1987. Role of fire in the seed germination of woody taxa in California chaparral. *Ecology* 68, 434–443.
- Konar, R., Roberts, C., 1996. Large scale landslide effects on two exposed rocky subtidal areas in California. *Bot. Mar.* 39, 517–524.
- Ladah, L.B., Zertuche-Gonzales, J.A., Hernandez-Carmona, G., 1999. Giant kelp (*Macrocystis pyrifera*) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998. *J. Phycol.* 35, 1106–1112.
- Larson, R.J., DeMartini, E.E., 1984. Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. *Fish. Bull.* 82, 37–53.
- Moreno, C.A., Jara, H.F., 1984. Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fuegian Islands, Chile. *Mar. Ecol. Prog. Ser.* 15, 99–107.
- Nelson, P.A., 2001. Behavioral ecology of young-of-the-year kelp rockfish, *Sebastes atrovirens* (Pisces: Scorpaenidae). *J. Exp. Mar. Biol. Ecol.* 256, 33–50.
- Neushul, M., Haxo, F.T., 1963. Studies on giant kelp, *Macrocystis*. 1. Growth of young plants. *Am. J. Bot.* 50, 349–353.
- Ott, R.L., Longnecker, M., 2001. An Introduction to Statistical Methods and Data Analysis, 5th ed. Duxbury, Pacific Grove, CA.
- Persson, L., Eklov, P., 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76, 70–81.
- Pierce, S.M., Cowling, R.M., 1991. Dynamics of soil-stored seed banks of six shrubs in fire-prone dune *Fynbos*. *J. Ecol.* 79, 731–747.
- Reed, D.C., Lewis, R.J., 1994. Effects of an oil and gas-production effluent on the colonization potential of giant kelp (*Macrocystis pyrifera*) zoospores. *Mar. Biol.* 119, 227–283.
- Reed, D.C., Laur, D.R., Ebeling, A.W., 1988. Variation in algal dispersal and recruitment: the importance of episodic events. *Ecol. Monogr.* 58, 321–335.
- Reed, D.C., Anderson, T.W., Ebeling, A.W., Anghera, M., 1997. The role of reproductive synchrony in the colonization potential of kelp. *Ecology* 78, 2443–2457.
- Reed, D.C., Schroeter, S.C., Raimondi, P.T., 2004. Spore supply and habitat availability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). *J. Phycol.* 40, 275–284.
- Savino, J.F., Stein, R.A., 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Am. Fish. Soc.* 111, 255–266.
- Schimmel, J., Granstrom, A., 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77, 1436–1450.
- Schmitt, R.J., Holbrook, S.J., 1990. Contrasting effects of giant kelp on dynamics of surfperch populations. *Oecologia* 84, 419–429.
- Schroeter, S.C., Dixon, J.D., Kastendiek, J., Smith, R.O., Bence, J.R., 1993. Detecting the ecological effects of environmental impacts: a case study of kelp forest invertebrates. *Ecol. Appl.* 3, 331–350.
- Sikkel, P.C., 1995. Diel periodicity of spawning activity in a permanently territorial damselfish: a test of adult feeding hypotheses. *Environ. Biol. Fish.* 42, 241–251.
- Steele, M.A., Anderson, T.W., 2006. Predation. In: Allen, L.G., Pondella, D.J., Horn, M.H. (Eds.), *The Ecology of Marine Fishes: California and Adjacent Waters*. University of California Press, Berkeley, pp. 428–448.
- Steele, M.A., Malone, J.C., Findlay, A.H., Carr, M.H., Forrester, G.E., 2002. A simple method for estimating larval supply in reef fishes and a preliminary test of population limitation by larval delivery in the kelp bass *Paralabrax clathratus*. *Mar. Ecol. Prog. Ser.* 235, 195–203.
- Stephens Jr., J.S., Larson, R.J., Pondella II, D.J., 2006. Rocky reefs and kelp beds. In: Allen, L.G., Pondella II, D.J., Horn, M.H. (Eds.), *The Ecology of Marine Fishes: California and Adjacent Waters*. University of California Press, Berkeley, pp. 227–252.
- Syms, C., Jones, G.P., 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81, 2714–2729.
- Tegner, M.J., Dayton, P.K., 1987. El Niño effects on southern California kelp forest communities. *Advances in Ecological Research* 17, 243–279.
- Tyler, C.M., 1996. Relative importance of factors contributing to postfire seedling establishment in maritime chaparral. *Ecology* 77, 2182–2195.